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BIVALVE LARVAL RESEARCH, IN TRANSITION: A COMMENTARY

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Substantial progress has been made in the complex, but rewarding study of the biology of planktonic molluscan bivalve larvae during the last four decades. This brief commentary is written at a time when, of necessity, we are moving from field to closed system molluscan mariculture. Presented in the interest of providing historical continuity and encouraging further creative research, I summarize some of the highlights of research, point out voids in knowledge, and touch on suggestions (some perhaps far out) for further inquiry on the biology of molluscan bivalve larvae.

Earliest ecological studies of bivalve larvae in the western hemisphere were conducted by Julius Nelson, Biologist at the New Jersey Experiment Station, with the assistance of his son, Thurlow, in estuaries on the east coast of New Jersey. Their pioneer work on seasonal distribution and movements of larvae of *Crassostrea virginica* (Gmelin) was begun in 1908 (Nelson 1909).

The first obstacle to be overcome by Julius Nelson was development of a method for sampling larvae. The prototype of the present day plankton net was probably first introduced by Johannes Müller in 1846 (Sverdrup et al. 1942). Nelson, although familiar with the prototype, was unable to use such a net because "the finest cloth has just about space enough between its meshes to permit the passage of the fry when they are full grown" (Nelson 1909).

With characteristic ingenuity, Nelson went to the use of Lautenschlager filter paper folded inside a chemical funnel. Early in the morning when the air was stillest, and the surface of the coves calmest, he dipped water from the surface into the glass funnel. After the water had almost filtered out, he held a tumbler below, and punched a hole through the bottom tip of the filter allowing the residue to drop into the glass. He then washed sediment and larvae from the filter paper through the hole into the tumbler. Although this was an effective procedure, it was extremely time consuming and limited sampling to surface waters.

By 1913 bolting cloth, fine enough to retain all stages of oyster larvae, was available from the Simplex Company, and Nelson started towing a plankton net. In addition, he devised a method for pouring measured quantities of surface water, as well as bottom water taken with a Moore sampler (a brass cylinder with a valve at each end), through the net to determine the vertical distribution of the larvae. Julius and Thurlow Nelson were thus able to make important contributions to the ecology of oyster larvae, and commenced identification of larvae of other bivalves in New Jersey estuaries as well. These technological advances may seem modest enough, yet without them investigation of the larval ecology of oysters would not have been possible.

Technological advances for the study of the distribution and movements of bivalve larvae in the field have been meager (Carriker 1967; Kasyanov et al. 1975; Scheltema 1975; Turner 1975; Mann 1986b). Spatial and temporal distribution are still monitored by pumping seawater into plankton nets from different strata in the water column. The laboriousness of this approach was amply demonstrated by Wood and Hargis (1971) in their ambitious, large scale, multiship study of bivalve larval transport in the James River. Continuous sampling with the Hardy plankton recorder is impractical near shore because of shallow turbid waters, and because the sampler screens primarily horizontal strata. Coulter counter-like devices could be used in conjunction with a pump to sample subsurface waters, but are not useful because they do not distinguish different species, and likewise sample only a single stratum per instrument. The research of Price et al. (1977) on automatic sorting of zooplankton could suggest a means for sorting bivalve veligers, but would be totally impractical in the identification of larvae even to the genus or family. The admirable investigations of Lutz et al. (1982) on the identification of bivalve larvae using hinge structures will insure accuracy, but will not permit rapid identification of species even in the laboratory. Counting plantigrade bivalves is still done by laborious examination and sorting under the microscope in sediments excised from the bottom. A method for "automated" sorting is urgently needed. Some of us in the past have experimented with techniques using density gradients (see also Sellmer 1956) and washing and screening (Coffin and Welch 1964), without startling results; and others are now experimenting with density gradient centrifugation, also not simple in practice. Perhaps an entirely different approach based on behavioral responses shortly after the time of collection in the field, can be devised to separate young bivalves from sediment samples. The use of larval traps (Carriker 1961) for determining the

density of pediveliger sets in the field has not received general acceptance. Innovations are critically needed in these areas of veliger and plantigrade samplings!

In the course of evolution behavioral mechanisms undoubtedly evolved that are based on estuarine circulation systems for retention of bivalve larvae within estuaries (Carriker 1967). Yet portions of estuarine larval populations can be transported onto the continental shelf by spring ebbings tides (Carriker 1961), carried on flooding tides into adjacent estuaries, swept from the shelf out into the deep ocean, or even dispersed long distances in the ocean (Mann 1983, 1986b). Scheltema (1971), for example, indicated that shipworm larvae can be carried by ocean currents across ocean basins. The question of what mechanisms stimulate larvae, like those of *Spisula solidissima* (Dillwyn) and *Arctica islandia* (Linné), to settle on specific bottoms of the continental shelf is still unanswered. These are intricate zoogeographic problems requiring investigation, particularly with reference to the fate of displaced larvae.

The behavioral and physiological mechanisms by which bivalve larvae maintain their vertical positions in the water are yet undefined. Evidence for mechanisms that could trigger selective swimming have not been experimentally demonstrated (Wood and Hargis 1971). The belief that velar activity continues throughout planktonic existence without cessation does not seem to be true in all cases. For example, the gas bubble described by Nelson (1928) suggests that at least one flotation device could exist that allows periodic rest; however, no one has yet shown how it is produced and maintained. Furthermore, although trochophores appear to swim continuously, many veligers (perhaps all?) alternate between periods of active upward swimming and periods of passive sinking with the velum either trailing or retracted within closed values (Mann and Wolf 1983; Mann 1986a; Carriker 1986).

Vertical distribution of swarms of larvae and patches of food microorganisms do not necessarily coincide in the water column. Whether larvae can identify and swim toward food particles has been questioned for some time. There is growing evidence, however, that some post-metamorphosed bivalves can preferentially ingest algae and reject particulate inorganic material in the pseudofeces (Kiørboe et al. 1980; Newell 1982), and can qualitatively discriminate among different kinds of food particles through rejection tracts on the palps (Shumway et al. 1985); whether bivalve veligers also can, is an intriguing possibility that awaits exploration. Mann (1986b) noted that the speed of active vertical (upward) movement of different species of bivalve larvae can range approximately from 1 to 10 mm/sec, which suggests that veligers could move relatively rapidly if attracted to metabolites from specific food microorganisms. Multivariate experimental studies determining larval response to levels of two or more simultaneously applied environmental factors have been carried out (see, for example, Cain 1973 on combined effects of temperature and salinity, and Bayne 1964 on light and gravity); that conditions of environmental factors at which parents develop gonads and spawn can influence the tolerance of embryos and larvae to these factors is unresolved (Cain 1973) and bear examination.

Acutely needed for field investigations is a method for continuously recording, three-dimensionally, the vertical position and density of bivalve larvae. On first thought, something like a computerized optical-electronic system might serve the purpose; I am told by colleagues, however, that looking for larvae acoustically in the field is not practical because of problems of size, appropriate frequency, and transmission qualities of sea water. A new approach being developed by M. Pleass and D. Dey (personal communication, College of Marine Studies, University of Delaware) employing laser doppler for studies with microscopic planktonic organisms does appear promising—we await further developments with much interest.

Another critical requirement in the field is for tagging large populations of bivalve larvae in order to follow their movements in the water and settlement onto the bottom. Tagging of laboratory spawned embryos with isotopes and discharging them in selected estuaries probably is feasible; but following tagged larvae in the open water could prove very difficult even with the resources of modern technology, because of dilution problems resulting from dispersal and losses from predation (Carriker 1961). Submersibles suggest the use of motion picture cameras with magnifying optical systems for investigating the behavior of pediveligers while settling. There are serious problems with this, though, resulting from the compromise of magnification and depth of field in camera systems—to say nothing of the extraordinary problem of discriminating among different species of bivalve larvae in mixed natural populations. Perhaps all that can be done until further technological advances are made is to study pediveliger behavior in the laboratory in artificial systems (Prytherch 1934; Cranfield 1973b), employing both pediveligers captured in the field (as did Prytherch 1934) and those cultured in the laboratory. These "simple" studies have been highly informative, and many more are worth conducting.

Evidence is growing to show that behavioral swimming responses probably guide bivalve larvae into the vicinity of their natural benthic habitat, where settling behavior directs them to available favorable sites. Random settlement of bivalve larvae on unsuitable substrata thus probably occurs less commonly (Carriker 1967; Crisp 1976; Gray 1974; Meadows and Campbell 1972). Crisp (1976) goes so far as to suggest that dispersal and habitat searching are part of an integrated pattern in which maintaining itself at a certain depth the larvae increases its chance of being carried in a favorable direction, light and gravity, among other factors, giving the larvae a reference orientation. Comparative field and laboratory studies on habitat selection (or on the behavior that results in bivalves being found in particular

places at particular times in nature—at best a difficult area of research) will have major importance in applied malacological ecology (Meadows and Campbell 1972).

The same may be said of investigations in controlled-environment (closed) mariculture (Carriker 1976). Before bivalves can be cultured efficiently and cost effectively their choice of habitat (Meadows and Campbell 1972; Crisp 1976), chemical and physical requirements (Bolton 1982; Gallagher and Mann 1986), preferred foods (Walne 1970; Epifanio 1976), extent of gregariousness (Hidu et al. 1978), and spawning (Morse et al. 1977) and settling (Morse et al. 1979) must be much better understood. Unfortunately, very few comprehensive studies have been made on even commercial species. Also it's possible there could exist species of bivalves other than those currently utilized that could serve as well, or better, in closed culture (Harry 1985). Lack of the planktonic larval stage in a species, for example, could be a major practical advantage; two species that come to mind are *Tiostrea lutaria;* and *T. chilensis,* which are ready to attach to the substratum upon release from the parent, thus bypassing the planktonic stage (Chanley and Dinamani 1980). Mann (1983) urges, however, that those contemplating culture of non-native species should consider carefully the potential spread of pest and disease organisms.

Many species of bivalves, as shown by extensive research on benthic communities are restricted to certain types of substrata. Nevertheless, little research has been done, especially among infaunal bivalves, to identify the chemical and physical features that attract pediveligers to specific substrata during settlement and metamorphosis. Initial studies were carried out by Keck et al. (1974) on factors influencing settling by *Mercenaria mercenaria* (Linné) and by Veitch and Hidu (1971) on the properties of a partially purified settling factor for *Crassostrea virginica.* Studies by Morse et al. (1977, 1979) have increased the predictability of spawning (using hydrogen peroxide) and settlement and metamorphosis (using chemical inducers). These chemicals are effective for a number of bivalves. There is a paucity of information on the optimal velocity gradients under which pediveligers settle, or their orientation with reference to currents during settling. We know that pediveligers search substrata for variable periods of time alternately crawling and swimming (Carriker 1967; Cranfield 1973b), but information is lacking on the time spent in these activities relative to different substrata, current velocity, temperature, salinity, suspended sediment, and competitors. Some species of plantigrades secrete a long byssus that carries young bivalves on relatively slow currents (Sigurdsson et al. 1976; Prezant and Chalermwat 1984). In other species, like *Ostrea edulis* Linné (Cranfield 1973b), the pediveliger in the laboratory employs an elaborate pattern of byssal attachments prior to cementing its shell to the substratum; whether a similar behavior is expressed in the field is unknown.

Uncommon success has been achieved in the laboratory culture to settlement of the larvae of many bivalve species (for example, Chanley and Andrews 1971). Primary credit for the pioneer investigations in this field in the United States goes especially to Loosanoff and Davis (1963), in Great Britain to Cole (1937), Bruce et al. (1939), and Walne (1963), and in Japan to Imai and Hatanaka (1949). A substantial part of this achievement was contingent upon the successful culture of several species of algae for feeding the larvae. It is probable that there exist other species of microscopic algal foods better suited for specific maricultural purposes than those currently employed; a high-temperature tolerant tropical flagellate, for example, has been found recently and is in current use (Ewart and Epifanio 1981). The advent more recently of plastic containers, screens, seawater tubing and other products greatly simplified the routine technological aspects of their work (Mann 1983). Invaluable, also, was the discovery that some bivalves can be conditioned to spawn out of season (Price and Maurer 1971; Gallager and Mann 1986b) permitting culture of larvae throughout much of the year. This practice is now applied in many hatcheries and laboratories with, for example, oysters, clams, and scallops. Bivalves not spawned by standard stimuli (thermal shock, addition of gametes, salinity and pH changes, exposure to hydrogen peroxide) can be induced to spawn by injection of serotonin (Matsutni and Nomura 1982), a procedure used successfully by Gibbons et al. (1983) to spawn the refractory *Arctica islandica* (Linné). These important collective successes have paved the way for the operation of hatcheries and the culture of bivalves in more or less controlled closed systems away from the sea (Dupuy and Rivkin 1972; Epifanio 1976, 1982; Dupuy et al. 1977; Castagna and Kraeuter 1981; Webb and Chu 1982; Wilson et al. 1984). Important research is in progress on identification of additional nutritional species of algae, combinations of nutritional species, manipulation of the chemical composition of algae through changes in cultural techniques, attempts to produce nutritional, formulated, encapsulated food particles (Epifanio 1976; Langdon 1983; Langdon and Bolton 1984), and the nutritional role of dissolved organic matter particularly free amino acids (Stephens 1982; Manahan and Crisp 1983). No artificial foods that nourish bivalve larvae as well as algae are yet available. I believe artificial feeds must be produced economically before commercial closed shellfish mariculture is successful. Addition of limited concentrations of particulate inorganic matter to laboratory cultures of bivalve larvae has been shown experimentally to improve growth in oysters (Ali 1982). The mechanism whereby this occurs is unclear but merits investigation in view of the ubiquitous suspension of particles that surrounds bivalve larvae in nature particularly in estuaries (Carriker 1986) and the suggested potential importance of silts in bivalve larval culture.

Successful laboratory cultivation of many species of bi-

valve larvae has opened unprecedent opportunities for multivariate experimentation in laboratory systems on behavior and movements in the water column of different bivalve larval stages in response to such ecological factors as gravity, salinity, light, temperature, pressure, external metabolites of algal food species, pheromones from parental adults, and chemicals from various kinds of bottom substrata. Such studies have begun to appear (for example, Haskin 1964; Bayne 1963, 1964, 1973; Hidu and Haskin 1978; Mann and Wolf 1983). This is a rich field for physioecological, behavioral experimentation, the results of which could be highly beneficial to closed as well as field mariculture of bivalves. Cultured larvae are also excellent subjects for the investigations of the effect of various fractions of oils, pesticides, and heavy metals (Mileikovsky 1970; Calabrese et al. 1973). The emerging technology of closed aquatic systems should make possible long-range studies of the effects of sublethal concentrations of these chemicals. Information thus gained, however, should be applied to natural field systems with caution until we know better whether laboratory culture modifies the tolerance of larvae to pollutants.

Significant studies of the macromorphology, microstructure, physiology, behavior, and biochemistry of bivalve larvae are appearing with increasing frequency. Notable, by way of examples, are publications of Cranfield (1973a, b, c, 1974, 1975) on glands of the foot and mantle folds of the pediveliger relative to settlement; Cragg and Nott (1977) on statocysts; Carriker and Palmer (1979) and Waller (1981) on the valves; Elston (1980) on soft tissues; Crisp (1967) on chemical factors and settling; Holland and Spencer (1973) on biochemical changes; Bayne et al. (1975) on effects of stress; and Gallager and Mann (1981) on lipid staining as an indicator of health. These investigations have established a noteworthy trend for structural-functional studies in bivalve larvae which will enhance basic and applied larval malacology.

Since the pioneer investigations of the Nelsons during the early years of the century, new substantive knowledge on bivalve larvae has been appearing at scientific meetings and in technical journals at an accelerating rate. This augurs well for future advances required to accomodate the difficult, but necessary, shift from field to closed system bivalve mariculture—a move necessitated by the growing inhospitality of conditions in coastal waters. This urgent trend requires essential new biological and technological information beyond what is now available. Studies touched upon briefly in this commentary suggests some areas deficient in information as well as some new directions for research. I have drawn attention to them to stimulate further creative basic-applied research on bivalve larvae and associated technology requisite for a successful transition in bivalve molluscan mariculture.

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FIELD STUDIES OF BIVALVE LARVAE AND THEIR RECRUITMENT TO THE BENTHOS: A COMMENTARY

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ABSTRACT A list of factors influencing the recruitment of bivalve larvae might include, but not be limited to, the following: egg quality, physical environment, food availability, loss to predation and disease during larval development, interplay of passive dispersal (horizontally) by water currents and depth regulation by active swimming, proximity of suitable and available substratum as metamorphic competency is achieved, and availability of sufficient metabolic reserves to complete metamorphosis to the benthic form. While tractable methods exist to quantify aspects of certain members of the above list, the focus of such work has usually been biased towards laboratory experiments or hatchery production. The purpose of this commentary is to suggest that a refocussing of efforts in bivalve larval biology on natural systems is both timely and needed

KEY WORDS: Bivalve larvae, recruitment

COMMENTARY

There is no question that laboratory work has allowed us to make many advances in the understanding of bivalve larval ecology; however, this work has often focussed on the culture of bivalves for economic purposes rather than examination of interesting ecological questions per se. Indeed, it was the intent of the original "laboratory" work of Brooks (1890) not to provide greater understanding of the ecology of oyster larvae but to provide a culture method for that species so that a repopulation of the Chesapeake Bay could be effected. Nonetheless the products of years of laboratory work suggest that we should again seriously consider field programs to examine larval biology and recruitment to the benthos. After several years of editing the *Journal of Shellfish Research* and even more years of reading the literature relating to bivalve larval biology an impression remains that the option for intensive field work is usually countered by comments such as: "too difficult, too much variability, too little control, and too time consuming." Consequently, we remain in the laboratory.

A list of factors which influence recruitment—here defined as successful metamorphosis from the pelagic pediveliger larva (sensu Carriker 1961) to the benthic, generally attached, feeding juvenile—of bivalve larvae might include, but not be limited to, the following: egg quality as influenced by the availability of food to the parent organisms, physical environment and food availability during larval development, the interplay of passive dispersal (horizontally) by water current and depth regulation by active swimming, loss to predation and disease, proximity of suitable and available substratum as metamorphic competency is achieved, and availability of sufficient metabolic reserves to complete metamorphosis to the attached benthic form. The list is not intended to be definitive or infer that the factors are listed in order of importance. It is, however, comprehensive. I wish to proceed through this list and demonstrate that we have the ability to quantify (to a variable degree) all of these factors. Consequently, it seems reasonable to suggest that we attempt such a quantification in a known field situation as part of a comprehensive examination of larval survival. I know of no case where this has been attempted for bivalve larvae.

The first item to be considered is egg quality. It has been documented for some time that a strong relationship exists between broodstock condition and larval viability in the flat oyster, *Ostrea edulis* L. (Helm, Holland and Stephenson 1973). More recently, Gallager and Mann (1986) have demonstrated similar strong relationships between broodstock condition and lipid contents of eggs in both *Mercenaria mercenaria* L. and *Crassostrea virginica* Gmelin. We offer a simple technique, based on the lipid specific stain Oil-Red-O, for assessing egg lipid content. Although developed and used in both the laboratory and commercial hatcheries, there is no reason why this cannot be used for field collected specimens. Indeed, we examined bivalve larvae using this technique in a preliminary manner during a field study of larval distribution on the Southern New England Shelf in 1981 and found it tractable and informative.

The second item is the physical environment during larval development. There is a considerable volume of literature on this subject although it is not always presented in a manner that is easily interpreted when attempting to apply the laboratory generated data sets to field situations. The data should be examined and used in models of field situations. Here, I offer two such examples. Lough (1974) examined the data of Brenko and Calabrese (1969) on the influence of temperature and salinity on *Mytilus edulis* L. larvae using response surface techniques. Immediately evident from this approach is the optimal physical environment for growth and survival. Yet, this approach is rarely

used. It is simple to interpret these data in concert with temperature and salinity values from the field. By contrast the tabular data of Davis and Calabrese (1964) for *Crassostrea virginica* Gmelin and *Mercenaria mercenaria* L., although informative, are considerably more difficult to use. An alternative approach, one that I have used in modelling occurrence and growth of *Arctica islandica* L. larvae on the New England Shelf (Mann, 1986a), involves stepwise integration of such data into more complex models. I will address this in my discussion of larval dispersal later in the text. When discussing the physical environment for developing larvae it is also relevant to include the presence of toxic materials. These may originate from natural sources, for example the exudates of blooms of the microorganism *Phaeocystis pouchetii*, or from waste disposal activities. In coastal areas adjacent to urban development the latter can be alarming in volume and variety of composition. Nonetheless progress is being made by toxicologists in quantifying the impact of selected toxic materials on larval molluscs.

The third item is food availability. Even though we can culture larvae in the laboratory on diets of phytoplankton, there is still no definitive statement on what larvae can and cannot eat in the field. How do we determine if enough food is present? Examine a worst case scenario; exclude dissolved organic carbon (D.O.C.), which Manahan (1983a, 1983b) and Manahan and Crisp (1982, 1983) have shown to be available for use by invertebrate larvae, and exclude non-phytoplankton particulate organic carbon (P.O.C.). The latter may be considerable; for example, work by Hugh Ducklow at the University of Maryland has shown that in the upper Chesapeake Bay bacterial biomass may be equal to that of phytoplankton. This leaves only phytoplankton in our examination. If larvae can survive on this, they can certainly survive when all the other carbon sources are also made available to them. Mann (1985) offers a series of calculations examining food availability at a station on the New England Shelf—a station where chlorophyll *a* concentration is probably well below that of inshore and estuarine regions where oyster and clam larvae are expected to grow and metamorphose. The calculation is simple and the result suggests that an estimated standing stock of cell concentrations in the range 0.54 cells/μl (obtained using very conservative conversion factors) to 67.7 cells/μl (using more reasonable conversion factors) is present during the summer and fall in the waters of the shelf environment. With the exception of the lowest estimates (0.54 cells/μl) of food concentration there is generally enough food present for larval development based upon laboratory estimates of bivalve larval requirements (see Walne 1965; de Schweinitz and Lutz 1976; Lutz et al. 1982). In essence we need worry only about atypical rather than typical events with respect to food impacting larval survival. As an example here, I offer the "brown tide" phenomena which Southern New England and Long Island have recently experienced—essential monocultures of apparently unpalatable phytoplankton. My point, however, is that it is generally difficult to make an argument that food quantity is ever limiting to larval growth.

The fourth item is larval dispersal. Is this an active or passive process? I have recently addressed this subject (Mann 1986a) and reviewed the literature (Mann 1986b). In regions of intense vertical mixing the weak swimming ability of larvae is overwhelmed and dispersal is passive. Consequently, if you want to know where the water (and therefore the larvae) is going you must consult your friendly, local physical oceanographer. To quote Andrews (1979): "Usually hydrographic regimes have not been known or appreciated to plan sampling of larvae." Fortunately, the trend toward active development of programs in collaboration with physical oceanographers is changing rapidly. In coastal systems seasonal stratification can be intense irrespective of whether estuaries or the inner shelf is being examined. In such regions, larval behaviour, a component that can be easily quantified in the laboratory, can be important and is amenable to modelling. The models can also be tested for validity in the field. The point that I wish to make is that we can use simple laboratory experiments in conjunction with field data, both physical and biological, to build testable computer models of larval dispersal. Physical scientists are progressing in the development of three dimensional, finite difference models of currents and sediment transport in coastal regions (see Sheng 1983). The modelling of sediment particle dynamics has many analogies with the modelling of larval behaviour. The problem is large but tractable and we, as bivalve ecologists, should address it.

The fifth item is disease and predation. We have a host of methods to examine disease in the stressful environment of a commercial hatchery operation (see Elston 1984 and references therein). While not all of these can be easily utilized on field collected specimens, due to small numbers of larvae collected, observational techniques such as electron microscopy can be used and draw upon the data provided by laboratory culture procedures. Castagna (personal communication) comments that in laboratory cultures significant numbers of larvae fail to metamorphose or develop very slowly. In the field these larvae would have increased susceptibility to predation. In a review by Gibbons and Blogaslawski (in press) a listing of predators on larvae include *Aurelia, Balanus, Brevortia, Chrysaora, Chthalamus, Diadume, Mnemiopsis, Noctiluca, Polydora, Sphaeroides* and a host of filter feeding bivalves and fish. Such impacts are potentially quantifiable using a combination of laboratory experiments and field collections. It would be particularly profitable here to coordinate efforts with larval fish ecologists (whose activities are considerable in the coastal regions) interested in fish feeding, diet and stomach contents.

The sixth item is substratum availability. Certain bi-

valves, notably oysters, exhibit substratum specificity. While the practice of provision of substratum to enhance settlement of commercially valuable bivalves can be traced back to Roman times and the writings of Plinius, and has been practiced extensively since the 1850's on the U.S. east coast, surprisingly (appallingly) little quantitative information exists on the fate of that substratum, over time, and its availability as a substratum to oysters in the face of competition for that substratum by what we term "fouling" species. In 1985 Richard Rheinhardt and I attempted to quantify the temporal and spatial development of fouling communities on clean shell substratum in the James River, Virginia. Our focus was, in part, to provide managers with a time window for optimal planting of shell to maximize oyster larval settlement and minimize prevention of settlement by fouling organisms. We used point sampling techniques to quantify our data—again illustrating that we must be prepared to look outside of our classical discipline to seek guidance from others in developing our field. The resultant manuscript is in review; however, to summarise, we illustrate that differences in rate of development and extent of areal coverage of fouling communities can be quantified. We also demonstrated that changes in the community structure could be elucidated using detrended correspondence analysis (Hill and Gaugh 1980). Examination of the predominant fouling species over time can give some insight into their potential impact on settlement of bivalves on adjacent, available substratum.

The final item is the assessment of whether or not morphologically competent-to-metamorphose larvae have sufficient energy reserves to complete that same metamorphosis. It is now accepted that metamorphosis is an energy consuming and thus critical period of the life cycle for a multitude of marine fishes and invertebrates. The importance of lipid reserves to this process in bivalves has been reported by Gallager, Mann and Sasaki (1986). As with egg quality we demonstrate that larval quality, including pediveliger larvae, can easily be assayed using a lipid specific stain. As I noted earlier, this technique is both simple and quantifiable. It can and has been used in the field and on other species. We have no excuse not to examine the viability of larvae in the field.

In summary then, I hope that this commentary has convinced you that we have at our disposal viable methods to examine many of the factors influencing larval survival and recruitment in the field. It is time to address the problem at hand.

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AN EVALUATION OF HEMOLYMPH DIAGNOSIS FOR DETECTION OF THE OYSTER PARASITE *HAPLOSPORIDIUM NELSONI (MSX)*

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ABSTRACT Use of hemolymph to diagnose *Haplosporidium nelsoni* (MSX) infections in the oyster *Crassostrea virginica* was evaluated by comparing results obtained from both fresh and fixed/stained hemolymph preparations with the standard histological method employing tissue sections. Fixed/stained hemolymph preparations detected 95–98% of all systemic infections, 58–64% of all subepithelial/local infections, and 30–33% of all epithelial infections that were found by tissue histology. Fresh hemolymph results were as reliable as fixed results for diagnosing advanced infections, but detected only 69% of light systemic infections and were only half as accurate as fixed hemolymph examination for more localized infections. Light infections were more difficult to diagnose in hemolymph samples taken during the early part of the infection period (August) than they were later (November), but there were no differences in detection accuracy associated with resistance or susceptibility to mortality caused by the parasite.

KEY WORDS: Parasite, diagnosis, hemolymph, *Haplosporidium nelsoni*, MSX, oyster, *Crassostrea virginica*

INTRODUCTION

Diagnosis of the parasite *Haplosporidium nelsoni* (MSX) (Haskin, Stauber, and Mackin 1966) in the American oyster *Crassostrea virginica* (Gmelin) is usually done by microscopic examination of fixed, stained tissue sections (Andrews 1966; Farley 1968; Newman 1971; Krantz et al. 1972; Ford and Haskin 1982). Although histologic detection provides considerable information about both host and parasite, it is time-consuming, expensive, and requires destructive sampling of oysters. A more rapid and less expensive method for detecting *H. nelsoni* would be a valuable alternative when speed is necessary, when a complete histology laboratory is not available, or when there is reason to keep the host alive for further sampling or experimentation.

In histologic section, plasmodial stages of *H. nelsoni* are seen in the circulatory system after they proliferate from initial sites of infection in the gill epithelium, indicating that the parasite should also be detectable in hemolymph samples and suggesting that hemolymph samples might provide a suitable means for diagnosis. In fact, *H. nelsoni* has been described in hemolymph collected from infected oysters (Farley 1968; Myhre 1969), but, to date, no systematic assessment of hemolymph diagnosis has been made (also, see Burreson et al. 1988).

To evaluate hemolymph diagnosis as an alternative to histology, we examined fresh and fixed/stained hemolymph samples for the presence and abundance of *H. nelsoni* and compared results with standard histological diagnosis of the same oysters. In addition, we determined the influence of infection intensity, season of collection, and level of resistance to *H. nelsoni*-caused mortality on the effectiveness of hemolymph diagnosis.

MATERIALS AND METHODS

Oyster Collections

Naturally infected oysters were collected in lower Delaware Bay at three times during the 1984–85 infection cycle (see Ford and Haskin 1982):

August 1984—onset of new infections;
November 1984—winter prevalence peak with established infections;
May 1985—spring prevalence peak with residual infections from previous summer's exposure.

Oysters were also categorized according to whether they had been selected for resistance to mortality caused by *H. nelsoni* (Haskin and Ford 1979):

Unselected—highly susceptible stocks, imported from outside Delaware Bay, or their offspring;
Delaware Bay natives—naturally selected wild stock of intermediate resistance;
Selected—laboratory-reared strains selected for resistance to *H. nelsoni*-caused mortality.

Oysters were kept in recirculating sea water at 12–14°C and 18–20 ppt salinity for 1–2 days before hemolymph was collected.

Hemolymph Diagnosis

The shell of each oyster was notched and hemolymph was collected from the adductor muscle sinus using a 1-ml

tuberculin syringe and a 25-gauge needle (Feng et al. 1971; Ford 1986). Hemolymph volumes of 0.1 or 0.2 ml were diluted to 1.0 ml in isosmotic sea water (19 ppt) and placed in a chamber constructed of a plastic embedding ring fastened by an elastic band to a glass slide (C. A. Farley, personal communication). Cells were allowed to settle for 20–30 minutes at which time the sample was scanned at 200× using an inverted microscope. A rough quantification of parasite abundance was made at this time:

Rating	*H. nelsoni*
0	None noted
1	Present, but sparse
2	Up to 10 per field
3	10 to 20 per field
4	More than 20 per field

After the fresh preparation was examined, the supernatant was drained, and the chamber removed. Attached cells were fixed in 3% glutaraldehyde or Davidson's fixative for 5 minutes and stained with Wright's stain. A minimum of 100 *H. nelsoni* plasmodia were counted in random 200× fields; however, at least 5 fields were counted regardless of number of parasites. Parasite concentration per milliliter of hemolymph was estimated from the number of fields examined, the settling chamber area, and the volume of hemolymph collected.

Histological Diagnosis

Preparation and examination of tissue sections followed Ford and Haskin (1982), and the infection rating scheme was a modification of theirs. Briefly, one 6 μm transverse section through each oyster was examined and infections were scored according to parasite abundance and location in the tissues:

Systemic—Parasites found in all tissues.
- Advanced—Averaging more than one parasite per 1000× oil immersion field;
- Light—Averaging fewer than one parasite per 1000× field but more than 100 per section;

Local—Parasites subepithelial, but localized in certain tissues, primarily the gill.
- Light—Averaging fewer than one per 1000× field but more than 100 per section;
- Rare—Averaging fewer than 100 parasites per section;

Epithelial—Parasites found only in epithelium, usually gill or palp.
- Light—Same as Local;
- Rare—Same as Local;

None—No parasites found.

Statistics

A total of 602 oysters was examined and classified according to month of collection, selection background, histologically determined infection level, parasites per milliliter of hemolymph as determined from fixed hemolymph preparations and/or the rating (0–4) obtained from fresh hemolymph examination.

Accuracy of hemolymph diagnosis was determined by comparing the number of cases in which hemolymph examination agreed with histological results in detecting either the presence or the absence of parasites. Results were further evaluated by comparing parasite concentrations in hemolymph from oysters with different histologically determined infection levels. The effects of season and selection for resistance on detection accuracy were assessed for fixed hemolymph samples using "G" tests of independence (Sokal and Rohlf 1981).

RESULTS

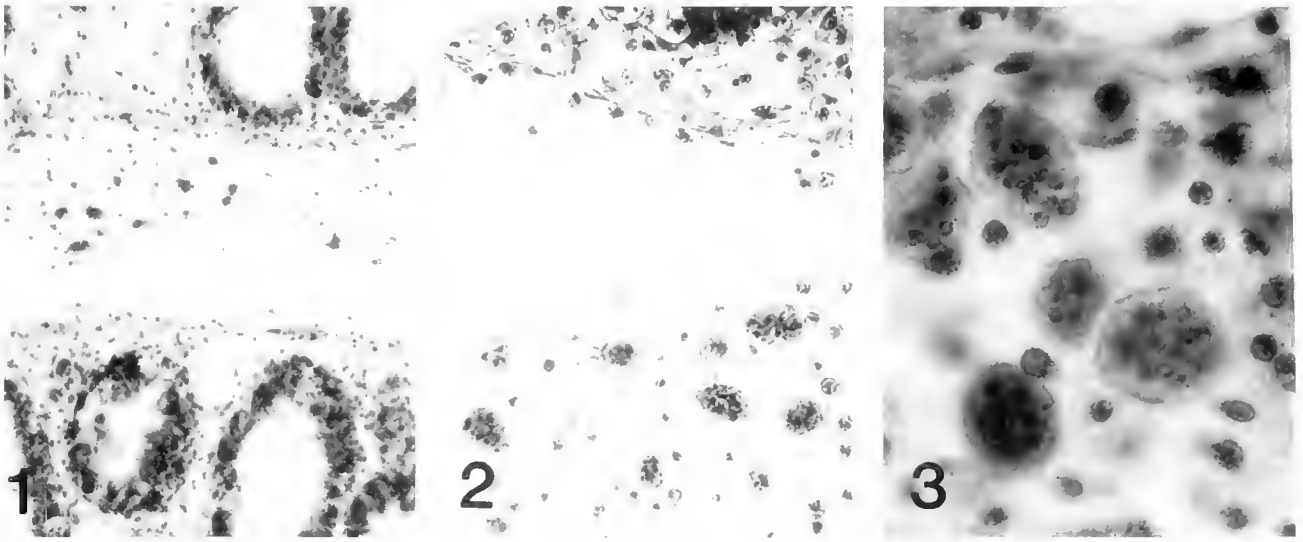
Appearance of Haplosporidium nelsoni in Hemolymph Samples

Histological sections show *H. nelsoni* in hemolymph vessels to be approximately spherical with clearly distinguishable nuclei (Figs. 1–3). In fixed hemolymph slides stained with Wright's stain, *H. nelsoni* plasmodia generally appeared as dense dark blue or purple bodies, approximately spherical, but occasionally showing extreme variability in shape (Figs. 4 and 5). They were clearly distinguishable from hemocytes in size, shape, and staining quality. Parasite nuclei were not often visible except in large plasmodia that had been flattened and disrupted by the cover slip.

Parasites in fresh hemolymph were also generally spherical, but sometimes displayed non-spherical forms (Figs. 6–8). They had a textured surface, a distinct plasma membrane, and were usually much larger than hemocytes. When parasites were of the same size as granulocytes, they could be distinguished because of the refractile granules in the latter (Fig. 7). Although they were capable of frequent and relatively rapid shape changes, parasites did not produce pseudopodia or filipodia, nor did they display locomotion characteristic of hemocytes. Outlines of parasite nuclei became visible after preparations had settled for half an hour or more.

Detection Accuracy in Hemolymph Compared to Histologic Preparations

Infections diagnosed as advanced by histology were detected in 97% to 98% of specimens also examined by fresh or fixed hemolymph (Table 1). Detection of Light/Systemic infections was equally good (95%) in the fixed hemolymph slides, but fell to 69% in fresh preparations. Localized infections, either Light or Rare, were detected with approximately 60% accuracy using fixed hemolymph, but only 17–32% accuracy in fresh preparations. Light or Rare/Epithelial infections were diagnosed in only 30% of the fixed hemolymph and 10–20% of the fresh hemolymph slides. Diagnoses of no parasites in fixed hemolymph agreed with histology in 80% of the cases, whereas this figure was 90% for fresh hemolymph preparations.



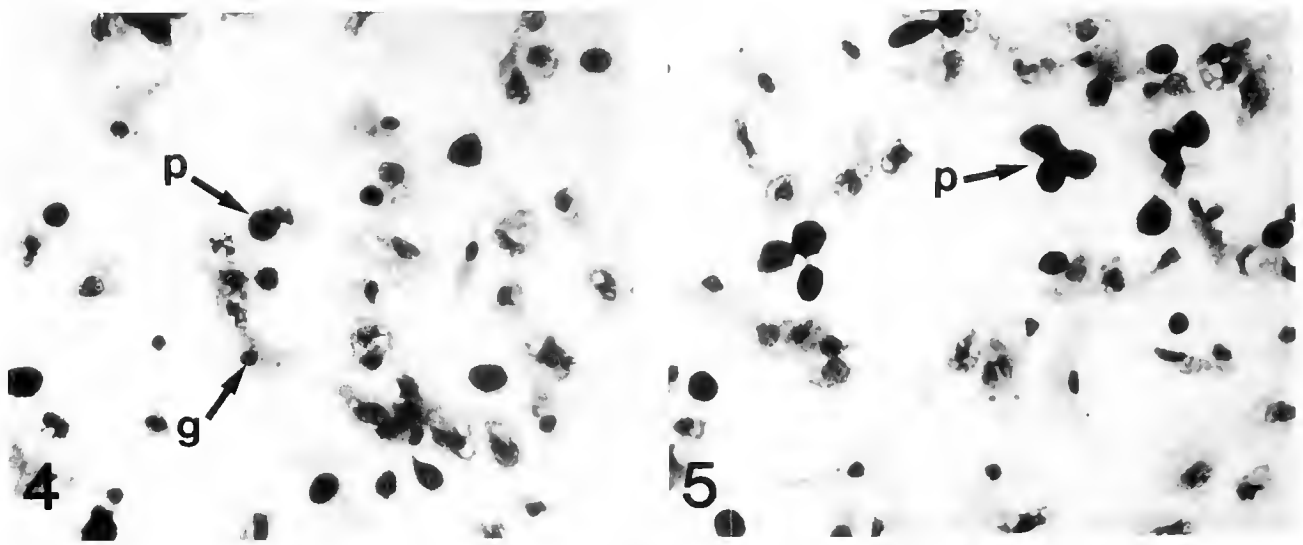
Figures 1–3. Histological section showing *H. nelsoni* plasmodia in hemolymph vessels. Figure 1. 100× Figure 2. Same field as Figure 1. 320× Figure 3. Several plasmodia with distinct, "capped" nuclei. 1000×

Parasite Concentration in Hemolymph Compared to Tissue Infection Levels

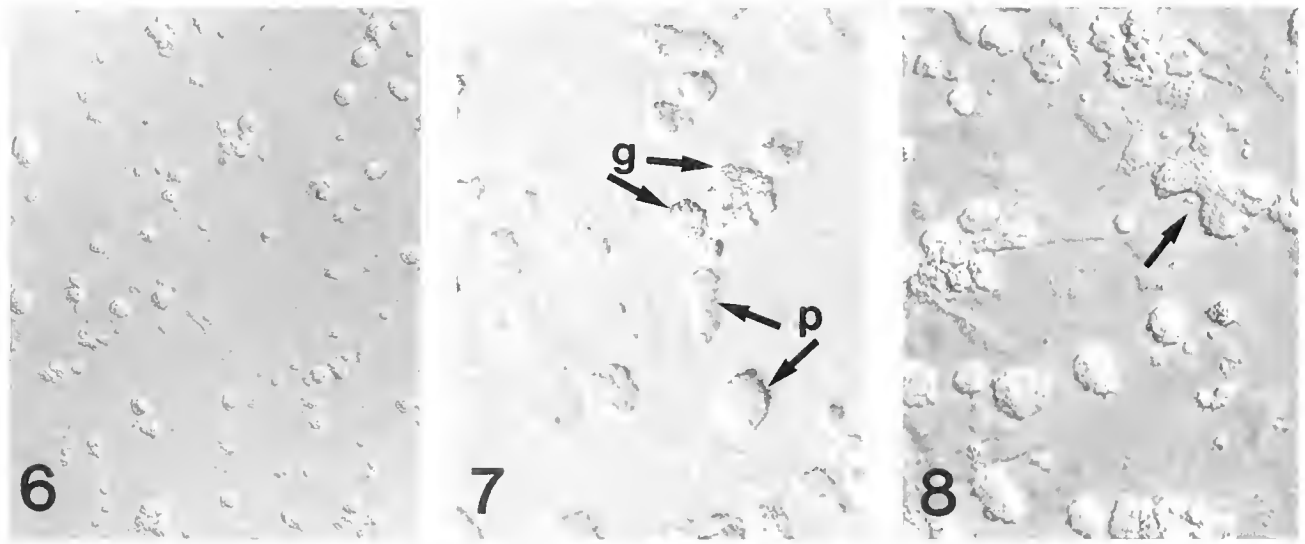
To determine how hemolymph parasite concentration related to tissue infection level, oysters in each tissue category were classified according to the estimated number of parasites per milliliter of hemolymph. Each class represented one log (base 10) increment ranging from 0 to 10^5 (Fig. 9 Fixed). Tests of independence were then performed comparing, between tissue categories, the fractional distribution of parasites in each hemolymph concentration class (Table 2). Advanced and Light/Systemic infections were significantly different from each other and from all other ratings. Differences in hemolymph counts became less significant as tissue infection intensities decreased, and no differences were found among the lightest categories and the None rating. For further examination, Light and Rare infections were combined in the Local and Epithelial categories, because there were no statistical differences between them.

The concentration of parasites in hemolymph, as estimated by fixed hemolymph slides, clearly paralleled their abundance in histologic section (Fig. 9 Fixed). In the None tissue category, 80% of the oysters had no detectable hemolymph parasites and an additional 10% had fewer than 100 per ml. Of the latter, most counts were extrapolated from only 1–2 parasites (or parasite-like cells) per slide, and could have been incorrect diagnoses. Nearly 10%, however, had concentrations of more than 100 parasites per ml, and several were in the 10^3 class.

Seventy percent of oysters with infections classed as Epithelial by histology, had no detectable parasites in hemolymph, and when they were found, virtually all concentrations were below 10^3/ml. The proportion of undeteeted in-



Figures 4 and 5. Plasmodia (p) and hemocytes (g) in a fixed, stained hemolymph preparation. 320×



Figures 6–8. Plasmodia in fresh preparation. Figure 6. Large, spherical plasmodia contrast in size and shape with smaller hemocytes, which are generally spread out on the slide. Nomarski differential interference contrast. 100× Figure 7. Spherical and non-spherical plasmodia. Note contrast between refractile granulocytes (g) and non-refractile plasmodia (p). Hoffman differential interference contrast. 320× Figure 8. Numerous plasmodia including a clover-shaped one in upper right corner (arrow). Hoffman differential interference contrast. 320×

fections fell to somewhat less than 40% in the case of Local infections, and again, positive samples generally had fewer than 10^3/ml. Among oysters with Light/Systemic infections, hemolymph parasite concentrations were about evenly divided above and below 10^3/ml, while Advanced cases were mostly above 10^4/ml. In the 2–3% of cases in which no parasites were found in the hemolymph of oysters diagnosed as having Advanced infections, notes taken at the time indicate that these individuals were gaping, that the hemolymph contained few cells and much debris, or both.

A similar increase in hemolymph parasite concentration with heavier tissue infection was found for fresh preparations although the pattern was less regular in the two Systemic categories than was found for fixed slides (Fig. 9 Fresh).

Association of Season and Selection with Detection Accuracy

To evaluate the effect of season and selection for resistance to mortality on detection accuracy, histological categories were combined as Systemic, Local, or Epithelial regardless of parasite abundance in the sections because percent agreement was statistically the same ($p > 0.05$) within each of these groupings (see Table 1). Within each combined category, percent agreement between hemolymph and histology was approximately the same regardless of selection history (Table 3). Local infections appeared to be least accurately detected in hemolymph in August, when infections were relatively new, and most accurately diagnosed in November when infections were better established (Table 3). Agreement for Systemic and Epithelial infections was approximately the same for all collection periods. Agreement for negative ratings was greatest in the earliest stages of infection (August) and least during the final stages (May).

Three-way "G" tests of independence were performed using percent agreement, tissue infection category, and either selection or season as variables (Table 3). Significant association was found between tissue infection intensity and both selection ($p < 0.01$) and season ($p < 0.05$), and between agreement and tissue intensity ($p < 0.01$), but not between agreement and either selection or season. There was, however, significant interaction between agreement, tissue intensity, and season ($p < 0.01$).

TABLE 1.

Agreement of fresh and fixed hemolymph preparations with histology for diagnosis of *Haplosporidium nelsoni* infections.

Histological Diagnosis	Hemolymph Diagnosis			
	Fixed		Fresh	
	Ratio[1]	Percent	Ratio[1]	Percent
Systemic				
Advanced	55/56	98	33/34	97
Light	35/37	95	11/16	69
Local				
Light	59/92	64	15/46	32
Rare	7/12	58	1/6	17
Epithelial				
Light	14/43	33	3/15	20
Rare	38/126	30	6/60	10
All infections	208/366	57	69/177	39
None	121/152	80	66/73	90
Total Examined	329/518	64	135/250	54

[1] Number of cases agreeing with histology/total in histological category.

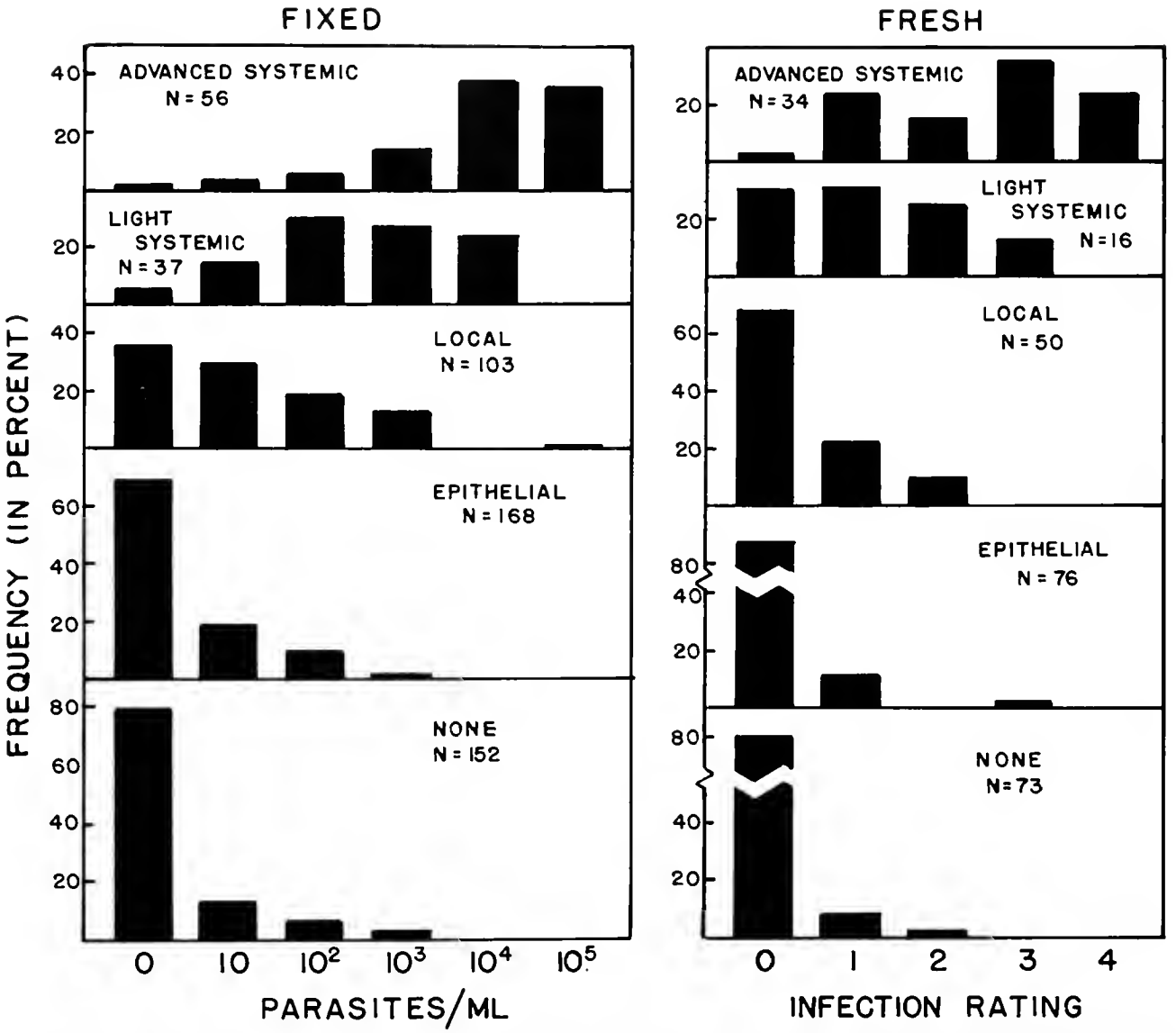


Figure 9. (FIXED) Frequency distribution of *Haplosporidium nelsoni* concentration in hemolymph, estimated from fixed/stained slides and grouped according to parasite levels in tissue sections. (FRESH) Frequency distribution of *H. nelsoni* infection ratings obtained from fresh hemolymph and grouped according to parasite levels in tissue sections.

DISCUSSION

The reliability of hemolymph diagnosis for detection of the parasite *Haplosporidium nelsoni* depends, not unexpectedly, on the severity of infection. Advanced infections can be detected with almost 100% accuracy, and equally well in fresh or fixed hemolymph samples. Hemolymph diagnosis will fail to detect a heavy infection only when an oyster is moribund, with inadequate hemolymph circulation to keep hemocytes and parasites in suspension. Lighter, more localized infections are more difficult to detect because there are few or no circulating parasites. In these cases, examination of fixed/stained hemolymph samples is generally about twice as accurate as that of fresh material. The lower accuracy of fresh hemolymph examination was because it was intended for rapid screening so less time was spent searching for parasites. Also, parasites were easier to distinguish from hemocytes when stained. Since the parasites were obviously present in the fresh preparations, additional time spent examining them, and perhaps increased recognition ability of the observer, would undoubtedly increase the reliability of this technique.

In a parallel study of oysters infected by *H. nelsoni* in lower Chesapeake Bay, Burreson et al. (1988) reported almost the same levels of agreement between hemolymph diagnosis and tissue histology as we found. Cooper et al. (1982) compared hemolymph screening with histology for diagnosis of soft clam, *Mya arenaria*, neoplasia and found that accuracy of diagnosis was related to disease severity, although overall correspondence of the two methods was

TABLE 2.

Results of "G" tests for independence to determine whether hemolymph concentrations[1] of *Haplosporidium nelsoni* differ according to tissue infection level.

	Tissue Infection Category						
	Advanced Systemic	**Light Systemic**	**Light Local**	**Rare Local**	**Light Epith.**	**Rare Epith.**	**None**
Advanced Systemic		N = 93 G = 34.68 p < 0.01	N = 147 G = 114.66 p < 0.01	N = 68 G = 35.40 p < 0.01	N = 98 G = 95.40 p < 0.01	N = 182 G = 163.17 p < 0.01	N = 208 G = 185.02 p < 0.01
Light Systemic			N = 128 G = 42.05 p < 0.01	N = 49 G = 15.95 p < 0.01	N = 79 G = 48.08 p < 0.01	N = 163 G = 84.50 p < 0.01	N = 189 G = 99.29 p < 0.01
Light Local				N = 103 G = 0.65 NS	N = 133 G = 14.85 p < 0.01	N = 217 G = 34.92 p < 0.01	N = 243 G = 48.90 p < 0.01
Rare Local					N = 54 G = 3.99 NS	N = 138 G = 4.92 NS	N = 164 G = 7.53 NS
Light Epithelial						N = 170 G = 7.97 NS	N = 196 G = 10.38
Rare Epithelial							N = 278 G = 6.26 NS
None							

[1] Parasite hemolymph concentrations were grouped in log (base 10) from 0 to 10^5 for each tissue category, then the distribution in each tissue category was compared by a "G" test for independence with the distribution in every other category.

much higher (94%) than was the case for *H. nelsoni* infections. Farley et al. (1986) found higher prevalences for the neoplastic condition using hemolymph diagnosis than when using histology, except in dead animals, from which suitable hemolymph samples could not be obtained. The higher sensitivity of hemolymph diagnosis for this disease compared to *H. nelsoni* is because neoplastic cells are of host origin. They may, in fact, stem from hematopoietic tissue (Yevich and Barszcz 1976), whereas *H. nelsoni* infective stages are encountered during feeding, and lodge and proliferate in the gill epithelium for variable periods before entering the circulation.

The choice of diagnostic technique for *H. nelsoni* depends on how the results will be used. For management purposes, either hemolymph method is entirely adequate for detecting infections that are advanced enough to cause immediate problems (i.e., days), but both have limited usefulness in finding early infections that would permit longer-range predictions (i.e., weeks or months) (see Ford and Haskin 1988). If hemolymph diagnosis is to be used in a monitoring program, results should first be evaluated against histology and occasionally validated in the same way during the course of the project. This is particularly important since the ratio of different infection types, as well as the accuracy of hemolymph diagnosis for each kind of infection, changes seasonally (Ford and Haskin 1982; this study).

For most purposes, we suggest that hemolymph diagnosis be made from fixed/stained slides, which are rapid and inexpensive to make compared to tissue sections. They do not have to be examined immediately, they can be prepared quantitatively, and can be saved for documentation. In certain cases, however, fresh preparations are entirely adequate and far more convenient. For instance, we routinely use this method to monitor the development of infections in groups of oysters to be used as a source of live *H. nelsoni* and to select individuals with sufficient numbers of parasites for *in vitro* experiments. To speed the process, we do not use chambers, but scan slides holding drops of hemolymph from several oysters.

It was not unexpected to find parasites in hemolymph samples from a number of individuals diagnosed as having no parasites in histological section, because we have always assumed that histological sections miss some light infections (Ford and Haskin 1982). In these cases, infections are detected by hemolymph diagnosis because the volume of hemolymph examined is much larger than the volume represented on a tissue section. The same explanation can be made for the parasites found in the hemolymph of 13% of the oysters with infections classed as Epithelial

TABLE 3.

Effect of selection for resistance to *Haplosporidium nelsoni*-caused mortality and season of collection on agreement of hemolymph diagnosis with tissue histology.

Infection Category	Selection Status						Month of Collection					
	Unselected[1]		Selected[2]		Del. Bay[3]		August		November		May	
	N[4]	%	N	%	N	%	N	%	N	%	N	%
Systemic	24/25	96	36/37	97	32/33	97	31/32	97	31/33	94	30/30	100
Local	11/17	65	23/37	62	31/50	62	27/56	48	27/31	87	11/17	65
Epithelial	13/39	33	24/75	32	16/58	28	31/91	34	14/50	28	8/31	26
None	38/50	76	58/75	77	25/27	93	62/72	86	38/50	76	21/30	70
Total	86/131	66	141/224	63	104/168	62	151/251	60	110/164	67	70/108	65

[1] Unselected = highly susceptible stocks, imported from outside Delaware Bay, or their offspring.
[2] Selected = laboratory-reared strains selected for resistance to *H. nelsoni*.
[3] Delaware Bay = native oysters with intermediate resistance.
[4] Number of cases in which blood and histological diagnoses agreed/total in histological category.

Results of three-way tests of independence. R = Percent agreement; C = Selection or Season; A = Tissue category.

		Selection		Season	
	DF	G	p	G	p
R × C × A independence	17	191.61	NS	192.24	NS
A × C independence	6	29.74	<0.01	13.30	<0.05
R × A independence	3	157.17	<0.01	157.17	<0.01
R × C independence	2	0.47	NS	2.18	NS
R × C × A interaction	6	4.24	NS	19.59	<0.01

by histology. Obviously, some infections that appear to be localized in tissue section are really systemic. Restriction of parasites to localized lesions is characteristic of strains selected for resistance to *H. nelsoni*-caused mortality in Delaware Bay (Myhre and Haskin 1970; Ford and Haskin 1987; this study). It was important to find no selection-related difference in correspondence of hemolymph and tissue diagnosis at any infection level, indicating that hemolymph diagnosis would give equivalent results for both selected and unselected strains.

The use of hemolymph in parasitological work is not limited to diagnosis, but may provide a means of obtaining live parasites for *in vitro* study. In such cases, the investigator would want to increase chances for collecting large numbers of parasites from heavily infected animals. The maximum concentration of parasites found in our study was 7.8×10^5 per milliliter of hemolymph. Feng (1965) demonstrated a linear increase in heart rate and numbers of circulating hemocytes with increased temperature, finding nearly twice the cell concentration at 22°C as at 12°C. We kept oysters at 12–14°C because reduced temperature prolongs survival of infected individuals; however, Feng's (1965) results predict that more than a million parasites per milliliter could be harvested from some individuals allowed to acclimate at higher temperatures before bleeding. In fact, preliminary tests in this study, performed on oysters collected in May and kept at 20°C or higher, found several individuals with parasite concentrations of more than one million per milliliter. Since the volume of hemolymph that can be collected from an oyster ranges up to several milliliters, several million parasites could be obtained from a single large, heavily infected individual.

Histology is still the most reliable detection method for *H. nelsoni* and provides more detailed information on the disease process than does hemolymph diagnosis; however, hemolymph diagnosis can be a very useful tool provided one understands its limitations. Hemolymph preparations can, in fact, contribute greatly to the study of host-parasite interactions, especially *in vitro*. Finally, hemolymph diagnosis is especially valuable because it permits repeated sampling from the same individual (Cooper et al. 1982; Farley et al. 1986; Ford 1986), so that the disease process can be studied and manipulated experimentally with minimum numbers of animals and with increased statistical control over individual variability.

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A COMPARISON OF PARAFFIN HISTOLOGY AND HEMOLYMPH ANALYSIS FOR THE DIAGNOSIS OF *HAPLOSPORIDIUM NELSONI* (MSX) IN *CRASSOSTREA VIRGINICA* (GMELIN)

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ABSTRACT Diagnosis of the oyster pathogen *Haplosporidium nelsoni* (MSX) by paraffin histology is compared with a technique in which hemolymph drawn from the oyster adductor muscle sinus is examined for parasite plasmodia. Oysters from seed beds of the James River, Virginia imported to an MSX endemic area in May, 1986 were sampled monthly through December, 1986 and in February, 1987. A sample of 25 oysters was bled each month and then processed for sectioning. Of the 200 oysters sampled, 89 (44.5%) were diagnosed as infected using histology and 61 (30.5%) were diagnosed as infected using hemolymph examination. All the heavy and moderate infections diagnosed by paraffin histology were also diagnosed by hemolymph, but only 64.3% of the light infections and only 43.5% of the rare infections were diagnosed by hemolymph analysis. However, 92.3% of the undetected rare infections and 60.0% of the undetected light infections were localized in gills and plasmodia had not entered the circulatory system. The hemolymph technique, which takes about 4 h, detected 89.7% of the systemic infections diagnosed by paraffin histology.

KEY WORDS: *Haplosporidium nelsoni*, MSX, oyster, diagnosis, techniques

INTRODUCTION

Traditionally, protozoan parasites of oysters have been diagnosed by paraffin histological techniques (Farley 1967; Andrews and Frierman 1974; Ford and Haskin 1982). This technique is accurate, but time consuming when rapid diagnosis is needed. Although promising new diagnostic procedures utilizing enzyme immunoassay, monoclonal antibody techniques and nucleic acid probes are under development in most areas of the world where oyster diseases significantly reduce the harvest, none are currently available. A simple, rapid technique for diagnosis of bivalve diseases has been developed by C. Austin Farley. The technique relies upon the presence of parasites in host hemolymph that occurs in systemic infections.

The purpose of this study was to compare diagnosis of *Haplosporidium nelsoni* (Haskin, Stauber and Mackin) through an annual infection period using traditional paraffin histology and hemolymph analysis. Because of a prolonged drought and record high salinity in the Chesapeake Bay, Virginia during 1986, oysters had the highest levels of *H. nelsoni* ever recorded. These high prevalences allowed good comparisons of the two techniques.

MATERIALS AND METHODS

Oysters were dredged in May, 1986 at Horsehead Rock in the James River, Virginia. Oysters from this rock are known to be highly susceptible to MSX and have been used as controls for over 25 years for disease monitoring programs conducted in Chesapeake Bay by the Virginia Institute of Marine Science and in Delaware Bay by Rutgers University. A 0.6 m by 1.2 m (2 by 4 feet) tray containing 378 oysters was suspended from a pier at VIMS in the lower York River, an MSX endemic area. Two additional trays of 400 oysters each were placed at the usual monitoring location about 1 km upriver. The MSX infection period typically begins in May each year (Andrews and Frierman 1974), therefore oysters for disease monitoring are transplanted to trays each year at that time. A sample of 25 oysters analyzed for *H. nelsoni* at the time of transplantation was negative for the parasite. Samples of 25 oysters were taken from the pier tray in late May and approximately every 30 days through November, 1986. No oysters remained in the tray after the November sample was removed so an additional sample in February, 1987 was taken from one of the other monitoring trays. All oysters were analyzed for the presence of *H. nelsoni* by both hemolymph analysis and paraffin histology.

Hemolymph Analysis

Immediately after sampling oysters from the tray, each oyster was numbered and the shell notched opposite the adductor muscle with a hand-held grinding tool. Using a 22 ga needle, 0.1 to 0.2 ml of hemolymph was drawn from the adductor muscle sinus into a 3 cc syringe containing 2.0 ml of cold 15 ppt artificial seawater containing 0.05 gm/l phenol red. If too much hemolymph is withdrawn from the oyster a thick cell layer results after settling and the slide may be difficult to diagnosis. Contents of the syringe were gently expressed into Farley chambers and hemocytes allowed to settle for one hour. These chambers were developed by C. Austin Farley, NMFS, Oxford, Maryland and consisted of plastic tissue-embedding rings sanded flat to

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prevent leakage and held to numbered microscope slides with an elastic "pony-tail" band. Rubber bands are not satisfactory because they are easily cut by the edges of the glass slide. After one hour, chambers were removed and the slide with attached cell monolayer was fixed for 5 min in Dietrich's AFA. Slides were stained with Harris' hematoxylin and eosin, coverslipped, and examined for the presence of plasmodia.

Slides were initially scanned at 100× in their entirety or until plasmodia were observed. Later, plasmodia were counted in each of 5 100× fields randomly slected using a microslide field finder. In heavy infections five 450× fields were counted and converted to 100× counts by multiplying by a factor of 20. Average counts per five 100× fields are given in Table 1; a + symbol indicates that plasmodia were observed on the slide, but none was present in the randomly selected fields. Plasmodia counts could not be standardized to number of hemocytes because of high variability in number of hemocytes, even in uninfected oysters, and because heavy infections increased hemocytosis. Generally, there were relatively more hemocytes in heavy infections.

Paraffin Histology

After hemolymph was withdrawn, oysters were opened and an approximately 5 mm thick section of tissue through the visceral mass that included mantle, gills, stomach, intestine and digestive diverticula was excised and fixed in Davidson's AFA for 24 h. Tissue was embedded in paraffin, sectioned at 6 μm and stained with Harris' hematoxylin and eosin. Oyster tissue was not trimmed before or after embedding and sections from only one oyster were placed on each slide. Sections were diagnosed, without reference to hemolymph preparations, by technician Juanita Walker who has been responsible for MSX diagnosis at VIMS for over 20 years.

Rating of infection intensity was as follows: rare (R)-less than 10 plasmodia in entire section, not limited to gill epithelium; rare localized (RL)-rare to light infection restricted to gill epithelium; light (L)-less than 2 plasmodia per 450× field but greater than 10 in entire section; light localized (LL)-many plasmodia but infection restricted to gill epithelium; moderate (M)-2 to 5 plasmodia per 450× field; heavy (H)-greater than 5 plasmodia per 450× field; sporulation (S)-any infection when spores were present.

TABLE 1.

Comparison of prevalence and intensity of *H. nelsoni* in *C. virginica* determined by paraffin histology (P) and hemolymph analysis (A) in samples of 25 oysters. Hemolymph analysis values are average number of plasmodia per five 100× microscope fields.

Oyster number	27 May 86		27 Jun 86		29 July 86		28 Aug 86		25 Sep 86		27 Oct 86		1 Dec 86		27 Feb 87	
	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A
1	U	0	U	0	U	0	U	0	R	+	U	0	L	0	U	0
2	U	0	U	0	LL	0	L	10	U	0	U	0	U	0	H	55
3	U	0	U	0	U	0	U	0	RL	0	R	+	L	16	L	1
4	U	0	U	0	U	0	U	0	L	0	RL	0	U	0	U	0
5	U	0	U	0	U	0	RL	0	H	64	L	+	U	0	M	130
6	U	0	U	0	U	0	RL	0	U	0	U	0	RL	0	L	+
7	U	0	U	0	U	0	U	0	U	0	M	34	LL	0	L	3
8	U	0	U	0	H	384	U	0	U	0	U	0	L	3	U	0
9	U	0	U	0	H	528	M	8	U	0	R	1	RL	0	L	4
10	U	0	U	0	U	0	R	+	L	0	U	0	U	0	U	0
11	U	0	U	0	U	0	U	0	L	3	RL	0	L	18	M	+
12	U	0	U	0	U	0	L	0	M	7	U	0	U	0	RL	0
13	U	0	U	0	U	0	U	0	U	0	U	0	U	0	U	0
14	U	0	U	0	LL	0	U	0	H	161	U	0	L	2	L	+
15	U	0	U	0	U	0	U	0	L	1	R	3	R	+	L	+
16	U	0	U	0	LL	0	M	28	L	1	L	4	U	0	M	6
17	U	0	LL	0	L	3	M	20	L	0	H	1816	H	176	L	+
18	U	0	U	0	U	0	U	0	U	0	U	0	U	0	L	1
19	U	0	U	0	M	15	H	736	H	41	R	3	U	0	M	1
20	U	0	U	0	L	+	L	5	L	1	R	2	RL	0	L	3
21	U	0	U	0	U	0	L	2	R	0	R	+	LL	0	U	0
22	U	0	U	0	M	+	RL	0	S	+	M	52	LL	0	L	+
23	U	0	U	0	U	0	L	1	H	496	U	0	L	+	U	0
24	U	0	U	0	LL	0	U	0	U	0	R	+	U	0	U	0
25	U	0	U	0	RL	0	L	0	U	0	RL	0	LL	0	M	+
Total No. infected	0	0	1	0	11	6	14	9	16	11	15	12	15	7	17	16
Prevalence (%)	0	0	4.0	0	44.0	24.0	56.0	36.0	64.0	44.0	60.0	48.0	60.0	28.0	68.0	64.0

H = heavy; L = light; LL = light, localized; M = moderate; R = rare; RL = rare, localized; S = spores; U = uninfected; + = plasmodia present on slide, but none in random fields; 0 = no plasmodia on slide.

RESULTS

Of the 200 oysters analyzed for *H. nelsoni*, 89 (44.5%) were infected based on paraffin histology (Table 1). Prevalence of infection gradually increased through September and then remained at approximately 60% through fall and winter. Hemolymph analysis detected 61 infections in the 200 oysters (30.5%), or 68.5% of the total detected by paraffin histology. Hemolymph analysis detected all the heavy and moderate infections as determined by paraffin histology, but only 64.3% (27/42) of the light infections and 43.5% (10/23) of the rare infections. However, of the 15 light infections not detected by hemolymph analysis, 9 cases (60.0%) were localized infections and of the 13 undetected rare infections, 12 (92.3%) cases were localized infections (Table 1). Thus, hemolymph analysis detected 37 of the 44 (84.1%) rare and light systemic infections. As expected, no localized infections were detected by hemolymph analysis because plasmodia had not entered the circulatory system. If the localized infections are removed from consideration, hemolymph analysis detected 61 of the 68 (89.7%) systemic infections.

Plasmodia counts from hemolymph analysis sorted relatively well into rare-light, moderate and heavy infections, although there was some overlap (Table 2). Counts from hemolymph analysis for rare and light infections as determined by histology ranged from 1 plasmodium on the slide to about 5 plasmodia per 100× field, with much overlap between rare and light counts. Counts for moderate infections ranged from a few plasmodia on the slide to 130 plasmodia per 100× field and counts for heavy infection ranged from 41 to over 1800 plasmodia per 100× field. The oyster with spores in the digestive diverticula had a very low number of plasmodia in the hemolymph.

Size of plasmodia in hemolymph preparations depended upon the intensity of infection. In rare and light infections, plasmodia were usually small, between 5 and 20 μm in diameter, with 2 to 15 nuclei per plasmodium. In moderate and heavy infections plasmodia ranged from 5 to 70 μm in diameter and large plasmodia often had over 100 nuclei (Figure 1a). Most nuclei were about 2 μm in diameter with an obvious eccentric endosome and dark-staining bar of "Kernstab", but large metaphase nuclei, up to 11 μm long, were also present in many plasmodia. Plasmotomy appeared to be occurring in all large plasmodia and in many small plasmodia. This process appeared to commence with gradual concentration of cytoplasm in from two to seven areas at the periphery of the plasmodium (Figure 1b) with subsequent fragmentation of the original plasmodium into smaller plasmodia (Figure 1c). Plasmodia less than 15 μm in diameter were often observed in phagocytes.

TABLE 2.

Summary of hemolymph plasmodia counts for the four intensity categories determined by paraffin histology.

Paraffin histology intensity category			
Heavy	Moderate	Light	Rare
1816	130	18	3
736	52	16	3
528	34	10	2
496	28	5	1
384	20	4	+
176	15	4	+
161	8	3	+
55	7	3	+
41	6	3	+
	1	3	+
	+	2	0
	+	2	
	+	1	
		1	
		1	

DISCUSSION

Results of this study suggest that hemolymph diagnosis of *H. nelsoni* may be an acceptable and preferable alternative to paraffin histology diagnosis, depending upon the objective of the diagnoses. If a rapid survey of a large number of oysters is required for oyster mortality predictions, then hemolymph analysis is probably the technique of choice. All heavy and moderate infections and 84.1% of rare and light systemic infections were diagnosed by this technique. Similar results were obtained by Ford and Kanaley (1988) using hemolymph diagnosis. The hemolymph technique did not detect localized gill epithelial infections, but investigators disagree on the fate of these infections. If, as some believe, gill epithelial infections always develop into systemic infections, then the hemolymph technique may seriously underestimate the actual prevalence, and potential mortality, because localized gill infections may account for almost 50% of the infections in certain months (Table 1, July and December, for example). If, as others believe, gill epithelial infections do not develop into systemic infections, failure to detect localized infections may not be a serious disadvantage if the goal is to predict mortality. Unfortunately, until the life cycle of MSX is solved, there is no way to know if all systemic infections begin as localized infections in the gills. Thus, periodic calibration with paraffin histology should be incorporated into any monitoring program using hemolymph diagnosis.

The main advantage of the hemolymph technique is rapid diagnosis of *H. nelsoni*—approximately 4 h for a sample of 25 oysters as compared to more than 48 h for paraffin histology. The hemolymph technique may also detect other parasites, such as *Perkinsus marinus*, but no comparisons with paraffin histology or thioglycollate culture have been made for this parasite. The disadvantages of the hemolymph technique are primarily related to the fact that no permanent section of oyster tissue is obtained as it is in paraffin histology. Thus, there is no record of oyster tissue response to *H. nelsoni* infection and no record of

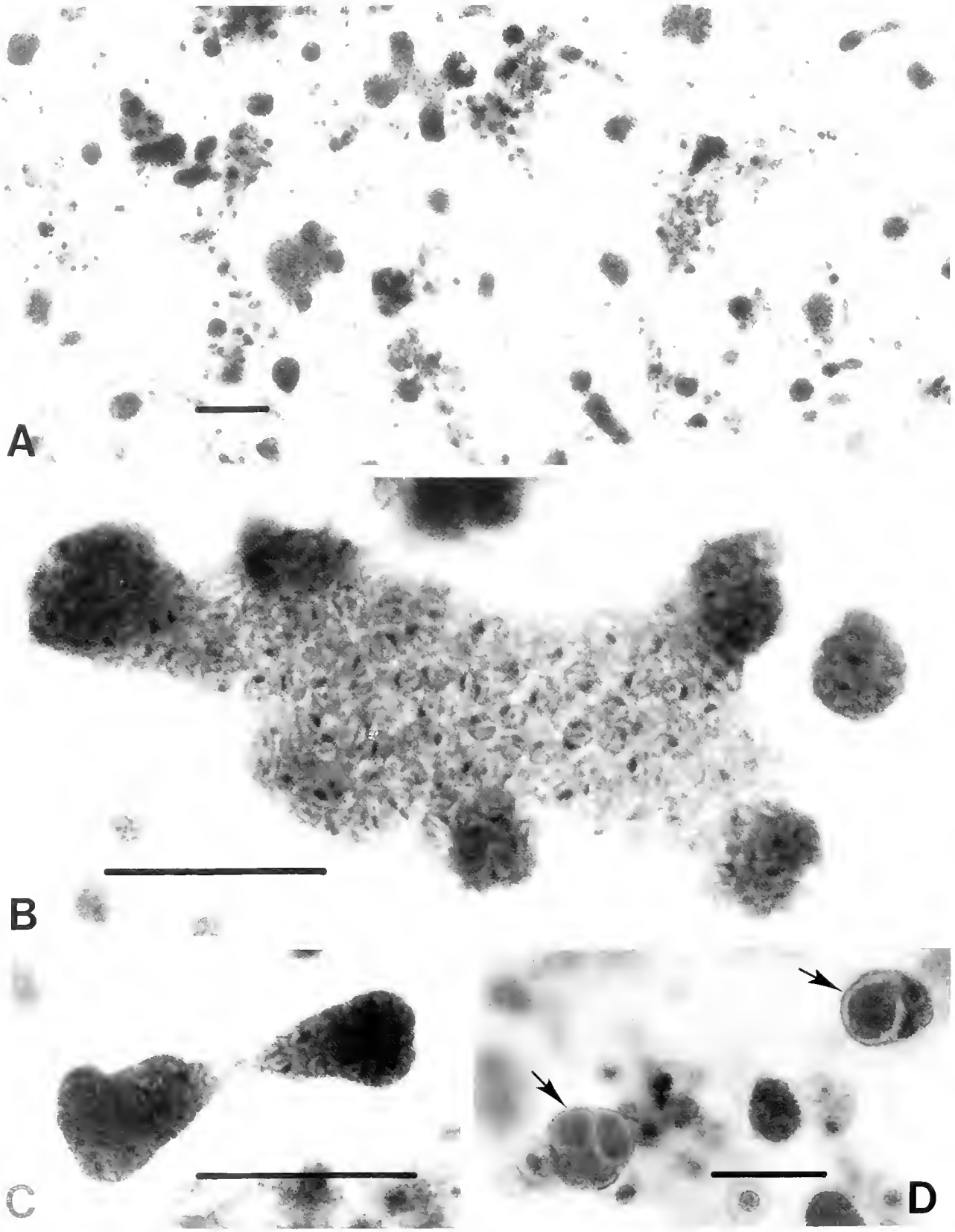

Figure 1. MSX plasmodia in hemolymph preparations. (A) Low magnification of heavy *H. nelsoni* infection illustrating various sizes and shapes of plasmodia. (B) A large plasmodium in the process of fragmenting. (C) Plasmodium that has almost completed separation into two smaller plasmodia. (D) Phagocytized plasmodia (arrows). The phagocyte on the left has engulfed at least two plasmodia. All bars = 20 μm.

other parasites present. These may or may not be important considerations, depending upon the objective.

The process of plasmotomy described may be an artifact of the technique in which plasmodia are allowed to settle onto a glass slide, but it clearly indicates that plasmodia are capable of fragmentation as suggested by Farley (1967).

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EFFECTS OF THE PARASITE MSX (*HAPLOSPORIDIUM NELSONI*) ON OYSTER (*CRASSOSTREA VIRGINICA*) ENERGY METABOLISM. I. CONDITION INDEX AND RELATIVE FECUNDITY

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ABSTRACT The effects of the endoparasite MSX (*Haplosporidium nelsoni*) on condition index and fecundity in the American oyster, *Crassostrea virginica*, were examined between May and November, 1985. On most sampling dates, mean condition index and mean relative fecundity were related to MSX infection intensity (uninfected individuals > epithelially infected individuals > systemically infected individuals). Overall, oysters with MSX infections confined to gill epithelium had a condition index that was 13% ($P < 0.02$) lower and a relative fecundity that was 35% lower than uninfected oysters. Oysters with systemic (general) MSX infections had a condition index that was 31% lower ($P < 0.001$) and a relative fecundity that was 81% lower ($P < 0.01$) than uninfected oysters. Reduced fecundity was manifested primarily as a reduction in the number of mature eggs produced rather than in the size of individual mature eggs. The observed reduction in fecundity is most likely the result of metabolic stress in which MSX reduces food intake and competes for energy reserves (reduces condition) which in uninfected individuals would be used for gamete production. Even at sublethal levels, MSX affects oyster fisheries by reducing meat yield and recruitment potential.

KEY WORDS: Oyster, parasite, MSX, condition, reproduction, *Crassostrea virginica*, *Haplosporidium nelsoni*

INTRODUCTION

In oyster biology, "condition" is a general term referring to meat quality that is most often assessed for economic reasons. However, condition is of physiological importance as well, being defined by Mann (1978) as "the ability of an animal to withstand an adverse environmental stress, be this physical, chemical or biological." The energetic advantage displayed by individuals in good condition is due to the fact that condition is directly proportional to the amount of glycogen contained in the tissues (Galtsoff 1964; Walne 1970). Glycogen is the primary energy storage substrate in oysters, providing energy for many physiological processes (Bayne 1976; Gabbott 1976, 1983).

Stored glycogen is clearly important as a source of energy for reproduction. Numerous studies have shown that glycogen is stored when food is abundant and later utilized in the production of gametes (Bayne 1976; Gabbott 1976, 1983). Fecundity, or the amount of gametogenic material produced, is directly related to the amount of glycogen accumulated prior to gametogenesis (Loosanoff 1965; Bayne 1975). Thus any stress that reduces condition (glycogen content) would also reduce fecundity (Bayne 1975).

The protozoan parasite MSX (*Haplosporidium nelsoni* [Haskin, Stauber and Mackin 1966]) has been responsible for mortalities of the American oyster, *Crassostrea virginica* (Gmelin), in Delaware and Chesapeake Bays since the late 1950's (Andrews 1966; Haskin et al. 1966; Haskin and Ford 1982). A typical pattern of infection leading to oyster mortalities has been described by Ford and Haskin (1982) and Ford (1985) as follows. New infections are acquired from June through October each year. Infections are initially confined to gill epithelium, where the plasmodia divide and proliferate, eventually breaking through the basement membrane. At this point infections rapidly become systemic as parasites are spread via the circulatory system. Ensuing mortalities occur in late summer and early fall as infections intensify. Infection levels are usually high over the winter, but mortalities lessen, most likely because of reduced metabolic activity of both host and parasite. Renewed parasite proliferation and oyster mortality accompany rising water temperatures the following spring. The high prevalence levels often recorded in late spring are from infections acquired the previous year.

Even though the epizootiology of MSX is fairly well understood, little is known as to how MSX affects the energy metabolism of individual oysters, eventually causing death. Newell (1985) found that oysters infected with MSX had significantly lower clearance rates than uninfected oysters and that this was correlated with a decline in condition index. Ford and Figueras (1988) described the pathological effects of MSX on gametogenesis. This paper reports the seasonal relationships that exist between condition, relative fecundity, and intensity of MSX infection in *C. virginica*.

MATERIALS AND METHODS

Oysters used in this study were from the 1980 and 1981 year classes produced as part of an ongoing experimental breeding program at Rutgers University (Haskin and Ford 1979; Ford and Haskin 1987), and were maintained in trays

intertidally at the Rutgers oyster hatchery located on lower Delaware Bay. Thirty individuals were examined six times between May and November, 1985 for condition index, relative fecundity, and degree of infection by MSX. Three additional samples were taken for the determination of relative fecundity and MSX level only. This interval of time was chosen because it is the period during which both reproductive and MSX activities are greatest.

The condition index used was that of Walne (1970):

$$\text{C.I.} = \frac{\text{Dry Tissue Wt. (g)} \times 1000}{\text{Shell Cavity Vol. (ml)}}$$

Oysters were cleaned of fouling organisms, measured (shell height), and the volume of water displaced by the whole oyster was obtained. A standard transverse (dorsal) tissue section of each oyster across gill, stomach, intestine, and digestive diverticula was removed and weighed (wet) prior to fixation for histological processing. The remaining tissue was weighed wet and then dried so that a dry wt./wet wt. ratio could be obtained and used to calculate the dry weight of the entire animal. The displacement volume of the two valves was measured and subtracted from the total displacement volume to obtain the shell cavity volume.

The histological procedures used for the diagnosis of MSX are those of Ford (1985). Tissue sections were fixed in Davidson's solution, dehydrated, cleared, and embedded in paraplast. Six-μm sections were stained with iron hematoxylin, acid fuchsin, and aniline blue. Each oyster was then categorized with respect to MSX infection intensity as either uninfected, epithelially infected (gills only), or systemically infected (subepithelial, general).

Since the oyster gonad is confined to a layer surrounding the digestive gland, relative fecundity (amount of gametogenic material) was obtained from the histological section as the ratio of [gonadal area/area of entire visceral mass] × 100, using an image analysis system (Bioquant). Measurements were made only on sexually differentiated individuals. This morphological approach to quantifying gonad production in oysters has been used previously (Mori 1979), and is more precise than measuring just the thickness of the gonadal layer (Loosanoff 1965).

In addition to the determination of relative fecundity, the diameters of 350 mature ova from oysters (collected 12 June) both uninfected (n = 7) and infected (n = 3) with MSX (both epithelial and systemic infections) were obtained from the histological sections using the Bioquant image analysis system.

Both condition index and relative fecundity values were

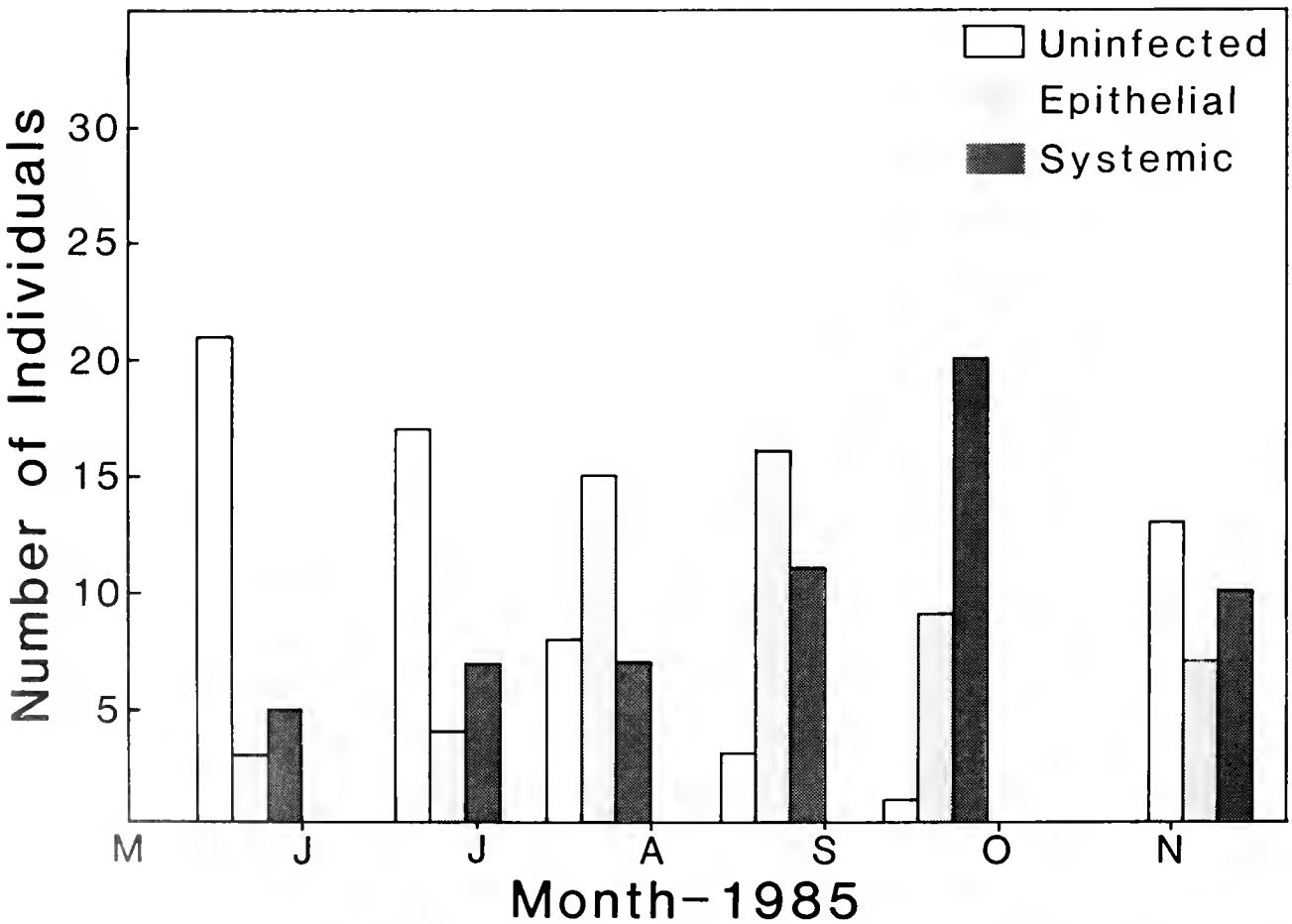

Figure 1. Number of individuals (*Crassostrea virginica*) within each MSX infection category at various times between May and December, 1985.

transformed (arcsin) prior to analysis (Zar 1974). Condition and fecundity were examined with respect to infection intensity and sampling date using a two-factor analysis of variance. To determine overall effects of infection intensity on both condition and fecundity, the means of differences (all sampling dates) between epithelially infected and uninfected oysters and between systemically infected and uninfected oysters were examined using a paired t-test (Zar 1974). Mean egg diameters were compared using a t-test.

RESULTS

Mean shell height ranged from 93 mm to 107 mm, and little growth occurred over the course of the study. Regression analysis demonstrated that over this size range, condition index and relative fecundity were unrelated to shell height.

The distribution of oysters within the respective infection categories reflected a typical progression of MSX infection in 1985 (Figure 1). Between May and September, the number of uninfected oysters within a sample decreased, and the number of oysters with both epithelial and systemic infections increased. Infections found in May and June were most likely acquired during the previous summer-fall infection period, or earlier. New infections became apparent in the July sample as an increase in the number of oysters with epithelial infections. Infection intensity generally increased from July through October. In November MSX prevalence and intensity was reduced.

Cumulative oyster mortality increased steadily throughout the study period (Figure 2). Mortalities occurring in May, June, and July were most likely the result of chronic infections. By November, cumulative mortality was starting to level off at about 50%.

Two-factor analysis of variance showed significant differences in condition index associated with both sampling date and infection category ($P < 0.005$). Mean condition index within each of the three infection categories generally increased between May and November 1985 (Table 1). In all months but August, when condition index was the same for both uninfected and epithelially infected groups, there was a reduction in mean condition index with increase in MSX infection intensity (i.e., the mean condition index of uninfected oysters > mean condition index of epithelially infected oysters > mean condition index of systemically infected oysters). Multiple comparison (Student-Newman-Keuls test) revealed that significant differences in mean

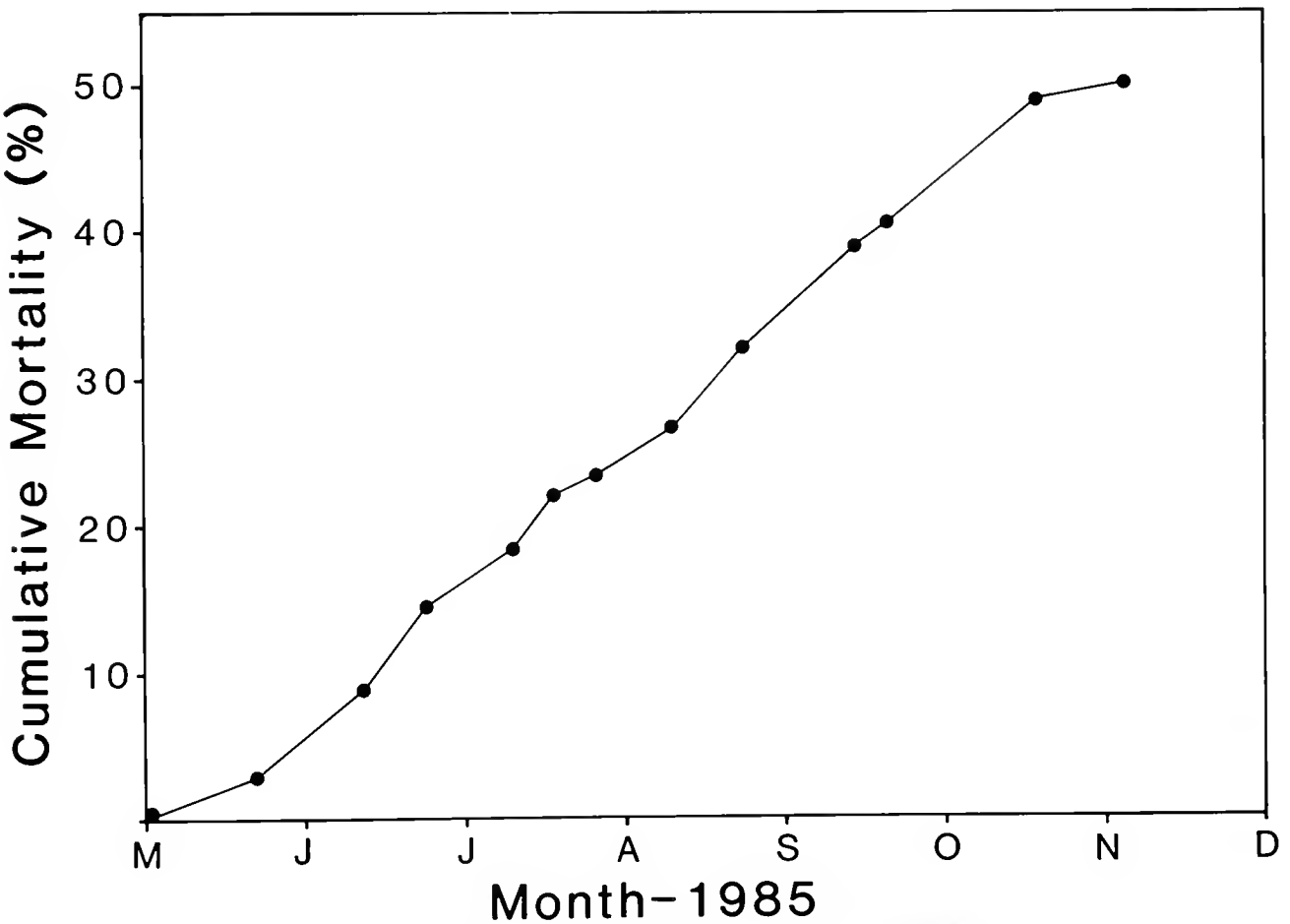

Figure 2. Cumulative mortality (%) of experimental oysters (*Crassostrea virginica*) between May and December, 1985.

TABLE 1.

Mean condition index (± 1sd) of oysters within each MSX infection category. Values not significantly different are connected by the same line

	Infection Category							
	Uninfected		Epithelial			Systemic		
Date	X	sd	X	sd	Δ%	X	sd	Δ%
21 May	75	5	56	4	−25	48	4	−36
25 June	71	2	62	3	−13	51	2	−29
22 July	103	1	84	2	−19	64	4	−37
22 August	91	1	92	4	+1	66	6	−28
19 September	107	—	100	3	−7	74	6	−31
6 November	119	4	102	5	−15	87	5	−27

TABLE 2.

Mean relative fecundity (± 1sd) of oysters within each MSX infection category. Values not significantly different are connected by the same line.

	Infection Category							
	Uninfected		Epithelial			Systemic		
Date	X	sd	X	sd	Δ%	X	sd	Δ%
21 May	21	5	9	7	−58	0	0	−100
12 June	30	1	19	2	−37	9	8	−71
25 June	18	5	8	4	−56	4	7	−76
9 July	6	6	12	5	+55	0	0	−100
22 July	8	6	6	5	−25	4	4	−51
9 August	6	4	4	3	−30	2	3	−71
22 August	0	0	4	5	—	0	3	—
19 September	21	—	0	2	−97	0	1	−100
6 November	0	0	0	0	—	0	0	—

condition index occurred between infection categories for all dates (Table 1).

A comparison of the differences in means between infection categories over the whole study period indicated that condition index was 13% lower in oysters with epithelial infection than in uninfected oysters ($P < 0.02$). Differences varied from 0 to 25% with smallest differences occurring in August and September, when most epithelial infections were of recent origin. Oysters with systemic infections had a condition index that was 29% lower than uninfected oysters ($P < 0.001$). These differences were relatively consistent (27–38%) over the whole period.

Two-factor analysis of variance also revealed significant differences ($P < 0.005$) in relative fecundity between infection category but not sampling date. Nonetheless, at all three levels of infection, relative fecundity was greatest in early June as maximum ripeness was attained and gradually decreased afterward as spawning proceeded (Table 2). The only exception was the single uninfected oyster in September, which had a ripe gonad. All reproductive activity had ceased by November in all infection categories. As was the case with condition index, relative fecundity was generally reduced with increasing infection intensity (all but 9 July and 22 August samples). It should be noted that the reduction in relative fecundity measured in this study (as a ratio) was due to a decrease in actual gonadal area (numerator) rather than due to an increase in total area (denominator). Multiple comparison (Student-Neuman-Keul) indicated that significant differences in mean relative fecundity between infection categories occurred on 21 May, 12 June, and 19 September (Table 2).

Comparing the differences between means of uninfected oysters and both categories of infected oysters for the entire study period indicated that relative fecundity was 35% lower in oysters with epithelial infections. Relative fecundity was 81% lower in oysters with systemic infections ($P < 0.01$).

The mean diameter of mature ova was 37.6 μm (s.d. = 5.9) in uninfected oysters and 35.9 μm (s.d. = 6.1) in oysters with MSX infections. These means were not statistically different ($P > 0.05$).

DISCUSSION

The indication that parasites stress their host, affecting a wide variety of biochemical and physiological functions is well documented (Lauckner 1983; Newell and Barber 1988). Although host/parasite relationships vary widely in their specifics, the stress to the host caused by parasitism generally has a nutritional basis (Thompson 1983). This can be manifested as altered food consumption, digestion, assimilation, and/or energy storage. With less energy available, host growth, including reproduction, is often impaired.

The primary metabolic substrate in marine bivalves is glycogen, and condition index is representative of the energetic state or health of an individual. A reduction in the condition of several bivalve species associated with parasitism has been reported. Infestation by *Polydora* caused a reduction in condition index in both *C. virginica* and *Mytilus edulis* (Lunz 1941; Kent 1979). *Crassostrea gigas* infected with *Mytilicola* had a lower condition index than uninfected individuals (Katkansky et al. 1967). Cole and Savage (1951) found that the flesh weight of *M. edulis* was reduced in relation to the number of parasites (*Mytilicola*) present. This was supported by Bayne et al. (1979) who found that high numbers of *Mytilicola* caused a depression in feeding rate and a reduced scope for growth in *M. edulis*, "which would result in time in a decline in condition."

The present study demonstrates that MSX reduces condition in *C. virginica* and that the reduction is related to the severity of the infection. Even though condition index varies seasonally, its proportional reduction in systemically infected oysters remains fairly consistent when measured

against uninfected oysters. The same is not true for oysters with gill epithelial infections, which have little or no depressing effect on condition index when they are newly acquired (August and September), but are associated with considerable reduction in condition as gill infections become older and more numerous (November–July).

Newell (1985) demonstrated that MSX infection was responsible for a significant reduction in the feeding rate of oysters. A reduction in incoming energy would in itself necessitate the utilization of stored reserves to meet metabolic requirements and result in a lower condition index (Newell 1985). A possible loss of feeding capability caused by MSX in epithelial infections (confined to gill tissue) may in itself be enough to lower condition index to the extent noted in the fall and spring samples. Another possibility is that infections diagnosed as epithelial may actually be systemic, with parasites located outside of the plane of section (see Ford and Kanaley 1988). The chances of this happening increase as gill infections become established, as they would be in the fall and spring samples. However, oysters with systemic (general) infections would be affected not only by a continued decrease in incoming food but by the metabolic burden of an increasing number of circulating parasites. Evidence of disrupted energy metabolism in oysters systemically infected with MSX is provided by Ford (1986) who found a drop in total serum protein concentration with increased infection intensity and Eble (1966) who found a considerable reduction in levels of digestive gland enzymes associated with MSX infection. Under prolonged negative energy balance, the result of reduced food intake, decreased digestive activity, and increased parasite metabolism, heavily infected oysters die at a greater rate than uninfected oysters. Mortalities could presumably result directly from the effects of MSX or indirectly from a decreased ability to resist predation or environmental stress.

By diminishing the total amount of nutrients available to the host at any time (both incoming food and stored reserves), parasitism might also reduce fecundity, or the amount of gametogenic material produced (Bayne 1975). Parasitism has been shown to affect bivalve reproduction both directly and indirectly. Cases of castration in which gametogenesis is directly inhibited has been reported for *Pecten alba, M. edulis,* and *Brachidontes recurvus,* all infested with trematode larvae (Uzmann 1953; Hopkins 1954; Sanders 1966). In other cases, effects are more subtle. The incidence of hermaphroditism in *C. virginica* increased as the result of infection with *Bucephalus* sp. (Tripp 1973). The gametogenic cycle of *M. edulis* was retarded, but otherwise unimpaired by *Mytilicola* (Williams 1969). Although not measured directly, a reduction in fecundity in *M. edulis* infected with *Polydora* was inferred by Kent (1979).

The results of this study show that fecundity in *C. virginica,* as measured by the ratio of germinal area to total area in a cross section of visceral mass, is reduced in relation to MSX infection intensity, and that this relationship is generally consistent over the entire MSX infection cycle, irrespective of reproductive state. A similar finding was reported by Ford and Figueras (1988) for oysters on the planted grounds of Delaware Bay. Ford and Figueras (1988) presented evidence suggesting that infected oysters showing clear inhibition of gametogenesis early in the reproductive period can recover from the disease and complete a delayed gametogenic cycle. The reduction in condition associated with parasitism shown by the present study, however, suggests that "recovered" oysters would still have relatively low energy reserves and might produce fewer gametes than individuals that had never been infected.

Stress has been shown to reduce fecundity in bivalves as the result of competition between maintenance metabolism, somatic production, and gamete production for the finite amount of energy made available from the diet (Bayne et al. 1985). Bayne et al. (1978) have shown that *M. edulis* produce fewer eggs having a lower energy content under conditions of temperature and nutritive stress, and that the reduction in fecundity is proportional to the level of stress. In the case of *C. virginica,* MSX reduces fecundity in relation to intensity (and duration) of infection. Egg size is probably reduced on average in individuals infected with MSX as a result of the delaying effect on the gametogenic cycle caused by MSX (Ford and Figueras 1988). However, there was no difference in the mean diameter of mature eggs (those most likely to be spawned) between oysters infected and uninfected with MSX, suggesting that the reduction in fecundity found in this study is primarily the result of a decrease in the number of eggs produced. A similar finding was reported by Barber et al. (1988) for a deep-water population of scallop, *Placopecten magellanicus,* thought to be nutritionally stressed.

Although MSX is often found in gonadal tissue as the result of systemic infection, only rarely does MSX directly destroy ripe gametes (Ford and Figueras 1988). Thus it appears that MSX affects reproduction in oysters indirectly by reducing available energy. This is most likely the result of a reduction in both feeding rate (Newell 1985), which reduces the ingested ration, and in reserves stored prior to the initiation of gametogenesis. With less energy available for gametogenesis (as reflected by reduced condition), fewer gametes are produced. Oysters with epithelial infections in May and June when maximum ripeness is attained not only have a reduced food intake but may have been more heavily infected the previous fall when nutrients were being stored. The greater duration of infection and associated metabolic burden presented by systemic infections reduce relative fecundity to an even greater extent.

The sublethal effects of MSX on oyster energy metabolism have potential implications for the oyster fishery. The loss in condition translates into a loss of yield (meat

weight). Even though condition is generally increasing in the fall when traditional harvesting begins, MSX prevalence can be high at this time and act to reduce condition. Secondly, Bayne (1975) has shown that larval growth and survival is adversely affected when the parents are stressed. Thus MSX may be responsible not only for a reduction in the number of gametes produced, but in the viability of those that are produced. In lower Delaware Bay, where MSX is enzootic (Ford and Haskin 1982), an associated reduction in spatfall might be expected. However, attempts to correlate MSX prevalence with spatfall have failed to detect any impact (Ford and Figueras 1988). This would be the case if most present-day larval production is from oysters in the upper seed beds, where protection from MSX is gained from reduced salinity (Haskin and Ford 1982). Even though we are currently unable to determine larval origins, the results of the present study suggest strongly that the contribution of lower bay (planted) oysters to overall recruitment in Delaware Bay is considerably diminished by the sublethal effects of MSX.

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POPULATION STRUCTURE OF THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*, ON AN OYSTER BAR IN CENTRAL CHESAPEAKE BAY: CHANGES ASSOCIATED WITH SHELL PLANTING AND INCREASED RECRUITMENT

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ABSTRACT An oyster bar near the Calvert Cliffs Nuclear Power Plant in central Chesapeake Bay contained very low densities of legal oysters, sublegals, and spat in 1979 because of poor recruitment during the 1970s. In the early 1980s, nearly 370 × 10^3 bushels of shell were planted in the area for cultch, and spat setting during five of the years between 1980 and 1986 was above average. Repeated spring and fall sampling from 1983 to 1986 of four areas within the bar by divers indicated that densities of legal oysters, sublegals, and spat had increased significantly to 4.8, 19.8, and 15.8 m^{-2}, respectively, or approximately 3, 33 and 150 times the densities estimated in 1979. A nested analysis of variance revealed only occasional differences among the four areas, although differences within the areas were common. Population size of the entire bar estimated at 5–7 × 10^3 bushels in 1979, increased at least fivefold to 36 × 10^3 bushels by 1983 and eightfold to 55 × 10^3 bushels by 1986. Increased oyster density on this bar demonstrates that management and shell planting can be effective mechanisms for increasing oyster yields when conducted during periods of high larval recruitment.

KEY WORDS: Oyster, *Crassostrea virginica*,, shell planting, larval recruitment, Chesapeake Bay

INTRODUCTION

The American oyster, *Crassostrea virginica* (Gmelin), inhabits Gulf and Atlantic coast estuaries as far north as the Gulf of St. Lawrence, but the Chesapeake Bay has traditionally been one of the major producers of oysters with commercial landings in Maryland as high as 688,500 m^3 (15 × 10^6 Maryland bushels) in 1885 (Kennedy and Breisch, 1981). A Maryland bushel equals 0.0459 m^3 or 2800 in^3. Landings have declined greatly, however, during the last century. From 183,600 m^3 yr^{-1} (4 × 10^6 bu) in the early twentieth century, landings declined to 82,600 m^3 (1.8 × 10^6 bu) by 1934; for the next 50 years, landings averaged 114,800 m^3 annually (2.5 × 10^6 bu). By 1983–85, however, the commercial catch was barely 45,900 m^3 yr^{-1} (1 × 10^6 bu), the result of near total recruitment failure during 10 of 14 years between 1966 and 1979, with only fair recruitment during the other 4 years (Krantz et al., 1982).

Although many factors enter into the success or failure of a particular year class (Kennedy and Breisch, 1981; Abbe, 1986), Ulanowicz et al. (1980) determined that larval recruitment in Maryland is closely related to sustained high salinity (>16‰) and the size of the oyster harvest the previous season. In general, the 4 years of fair recruitment between 1966 and 1979 were characterized by high salinity while salinity during the poor years was low. Above average salinity prevailed during 1980–82 and 1985–86, and high recruitment was observed in many areas of Chesapeake Bay in Maryland (Krantz et al., 1982; Krantz and Davis, 1983; W. Outten, Maryland Department of Natural Resources, Annapolis, Maryland, pers. comm.).

Although oysters are found throughout much of Chesapeake Bay, low population density or harvesting difficulty may limit the extent to which some areas can be worked. The Flag Pond oyster bar on the western shore of Chesapeake Bay near the Calvert Cliffs Nuclear Power Plant (CCNPP) was such an area prior to the early 1980s. The bar was included in the 1906–1912 Survey of Maryland Oyster Bars (Yates, 1913) and consists of 275 ha (680 acres), much of which is now shifting sand (inshore) or soft mud (offshore, depth >9 m), both unsuitable for oysters. Studies in 1968 (ANSP, 1968) and 1979 (Abbe, 1980) estimated a population size of 5–7 × 10^3 bu (based on 350 oysters per bushel) on about 81 ha of productive bottom (60–85 bu ha^{-1}). In some areas of the bar where oysters were found, however, many were attached to large rocks, effectively reducing the actual catchable density.

In 1980, 102 × 10^3 bu of shell were planted in the discharge area of CCNPP, and in 1982 another 197 × 10^3 bu were planted near Camp Conoy, both within the boundaries of Flag Pond bar. Subsequent spat sets near the plant were higher than recent averages, although 1980 (25–50 spat bu^{-1}) was just slightly better than during 1975–79 (0–10 spat bu^{-1}) (Davis et al., 1981). In 1981, the spat density was 140 bu^{-1} of material from natural bottom and 1060 bu^{-1} on planted shell (Krantz et al., 1982); the 1982 density was also over 200 spat bu^{-1} (Krantz and Davis, 1983). Because higher spat densities can lead to increased population densities and ultimately to higher yields of oysters, we began a program to determine the success of the shell planting and the newly settled spat over a multi-year period.

This paper presents the results of spring and fall surveys of Flag Pond bar during 1979 and from 1983 to 1986. It documents temporal changes in population structure and relates shell planting efforts to larval recruitment and sub-

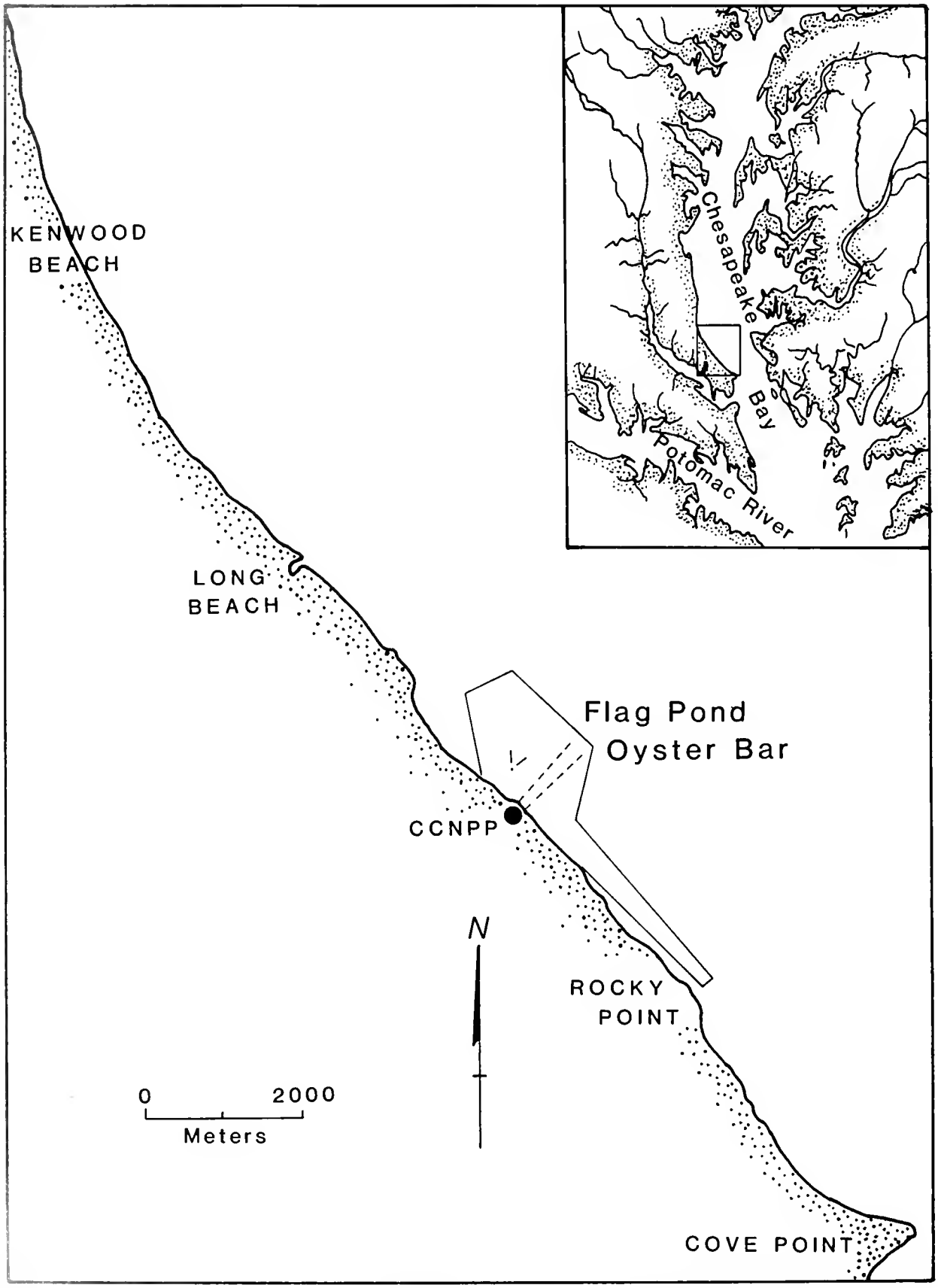

Figure 1. Location of Flag Pond oyster bar in central Chesapeake Bay adjacent to the Calvert Cliffs Nuclear Power Plant (CCNPP).

sequent commercial activity. It also demonstrates the value that shell planted at least 2 years can have for recruiting larvae.

MATERIALS AND METHODS

Description of Study Area

Flag Pond oyster bar is located 12 km north of the mouth of the Patuxent River on the western shore of Chesapeake Bay (Fig. 1); it is 4.4 km long and about 1.1 km wide at its widest point. The potential productive oyster bottom was estimated in 1979 to be 81 ha or 29% of the total area (Abbe, 1980). Much of the inshore bottom was littered with rocks eroded from the 30-m-tall cliffs along the shore, and oysters on this rocky bottom were difficult to harvest by conventional methods (hand tonging, patent tonging, and dredging).

Water depth over the bar ranges from less than 1 m to 10 m, but most of the oysters are confined to depths less than 8 m. Water temperatures range from near 0°C in winter to about 28°C in summer, and annual mean salinities generally range from about 10 to 15‰ (Abbe, 1983). Dissolved oxygen (DO) concentrations in summer range from 5 to 9 mg $O_2 l^{-1}$ in water less than 8 m deep, but are often 1 mg $O_2 l^{-1}$ or less in depths greater than 9 m. DO concentrations less than 3 mg $O_2 l^{-1}$ in shallow water occasionally occur for a day or so as a result of upwelling caused by west or southwest winds.

Sampling

The study was conducted from the 42-ft research vessel JOSEPH LEIDY during May–June and October–November 1979 and 1983–86 in the four areas outlined in Figure 2 selected from earlier mapping studies. Area 2 lay in the immediate discharge area of the CCNPP. It consisted of about 11.4 ha of shell-covered hard clay bottom and had shell spread on part of it in 1980. Area 4 (Camp Conoy) was 16.4 ha in size and had a sand, rock, and shell bottom; it received shell in 1982. Area 5 was a 19.5-ha continuation of Area 4. Its bottom was sand and shell, and it also had shell planted in 1982. A 4-ha tract at the common boundary of Areas 4 and 5 received an additional 70 × 10^3 bu of shell in 1984. All three areas were surveyed twice each year, and Area 6 was added to the 1983–86 surveys. Area 6 was a narrow 3.9-ha strip adjacent to and inshore of Areas 4 and 5. The bottom consisted of rock on hard clay, shell on sand, and sand. No shell was planted in this shallow area during the study.

Each area of study was outlined with buoys positioned with the aid of radar and LORAN C. Within each area a series of transects was made, with several points sampled along each transect. The LEIDY was anchored at a sampling location and three steel squares (each 0.33 m^2) connected in series by 2-m lines were thrown from each side so they spread apart and fell to the bottom. Water depth and

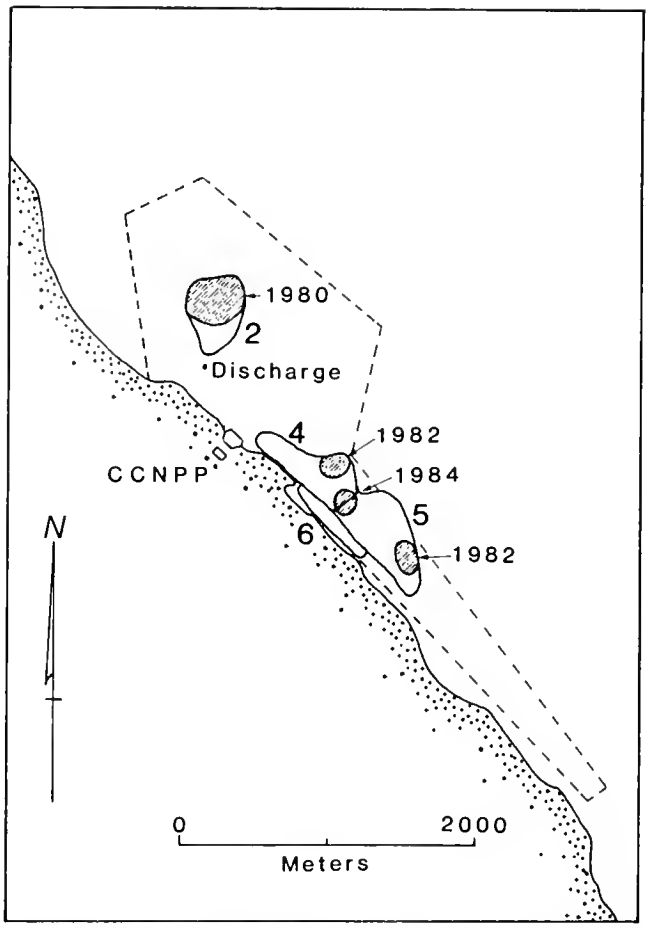

Figure 2. Outlines of areas sampled on Flag Pond during 1979 and 1983–86. Shaded areas show approximate areas and dates of shell planting.

turbidity prevented sight of the bottom from the LEIDY and thus prevented the bias that could have existed if the squares were deployed in clear water. These methods were similar to the random quadrat sampling by May (1971) in his survey of the Alabama oyster resources.

Divers removed all materials including oysters, shells, boxes (two attached empty shells), and rocks from each square and put them into nylon-mesh catch bags which were brought to the surface for examination. Shells and boxes were counted (except in 1979), and oysters were counted by size class: legal or 76 mm (3 inch) and over, sublegal, and spat. Sublegal oysters were those less than 76 mm that had set at least the prior year, and spat were oysters that had set during the present setting season (July–September). After all counts were recorded the LEIDY was moved to a new location and the procedure repeated.

The number of sample locations in each area varied according to areal size, but ranged from 9 (18 m^2) to 31 (62 m^2). May (1971) determined that a sample density of 2.06 m^2 ha^{-1} (1 yd^2 $acre^{-1}$) was sufficient to adequately sample the Alabama oyster population. During 5 years of the

present study we averaged 251 m^2 sampled annually on 51 ha (4.92 m^2 ha^{-1}).

Statistical Analysis

Data was analyzed using a nested analysis of variance (General Linear Model Procedure) (SAS Institute, Inc., 1982) in which all factors were assumed to be random. The model takes the form,

$$\log(\gamma_{ijkl} + 1) = \mu + \alpha_i + \beta_j(\alpha_i) + \gamma_k(\beta_j) + \delta_l(\gamma_k)$$

where

γ_{ijkl} = parameter measurement (number of shells, boxes, or oysters) for area$_i$, location$_j$, position$_k$, and replicate$_l$,
μ = overall mean,
α_i = area effect,
β_j = location-within-area effect,
γ_k = position (port or starboard)-within-location effect, and
δ_l = replicate-within-position effect

When significant differences among areas were detected ($p < 0.01$), a Student-Newman-Keuls (SNK) test was used to rank the areas according to their mean densities and determine where the differences occurred.

RESULTS

Densities of shells and boxes were highly variable from year to year, with shells increasing markedly after shell planting; e.g., in 1984, shells increased from 82 to 228 m^{-2} (Table 1), with some individual samples yielding 1000 m^{-2} or more. Boxes appeared numerous in 1983 (Table 1), but this resulted from one unusual sample (1 m^2) in Area 2 (1075 boxes) and three samples from Area 4 (249, 137, and 114 boxes) where very high densities of shells and sublegal oysters were found. Otherwise, the density of boxes in 1983 was similar to those of other years. In 1986 the density of boxes increased sharply from spring to fall during the second successive year of high salinity (Fig. 3).

Less variable than shells or boxes were the densities of legal oysters which increased each spring from the previous spring (Table 1) due to growth of sublegal oysters which reached 76 mm in length. Legal densities also increased from spring to fall each year for the same reason. Only in 1986 did the density of legal oysters decrease from spring to fall. Legal density of 1.7 m^{-2} in 1979 increased to 4.3 m^{-2} by 1983 as oysters that set in 1980 and 1981 began to reach legal size. Legal density peaked at 5.4 m^{-2} in 1985 before decreasing slightly in 1986.

Sublegal densities were fairly stable from fall of one year to spring of the next when recruitment was poor (1983 and 1984). When recruitment was good, however, as in 1985, the density of sublegals increased markedly the following spring as spat became part of the sublegal population (Table 1). Densities less than 1 m^{-2} in 1979 reached 33 m^{-2} in spring 1983 (Table 1) as a result of successful recruitment in 1981 and 1982, then decreased to 22 m^{-2} by fall 1983 as some oysters reached 76 mm and entered the legal class and others died.

The increase in legal density from spring to fall and the decrease in sublegal density during the same time seen in Table 1 was exhibited in each of the four individual areas (Table 2). Areas 4, 5 and 6, which were adjacent to each other, were similar in legal densities (4.6 to 5.4 m^{-2}), but far different in sublegal densities which averaged 34.3 m^{-2} in Area 5, 17.4 m^{-2} in Area 4, and only 4.7 m^{-2} in Area 6. In Area 2, adjacent to the CCNPP discharge, the mean

TABLE 1.

Densities of shells, boxes, and live oysters per m^2 collected during spring and fall 1979 and 1983–86 from Flag Pond bar.

	Area Surveyed (m^2)	Shells m^{-2}	Boxes m^{-2}	Legal Oysters m^{-2}	Sublegal Oysters m^{-2}	Spat m^{-2}
Spring						
1979	125	*	*	1.7**	0.8**	—
1983	105	64.3	18.9	2.7	33.2	—
1984	110	82.2	3.3	4.0	22.2	—
1985	182	135.2	1.4	4.9	17.2	—
1986	150	123.8	2.5	5.8	17.7	—
Mean	134	101.3	6.5	3.8	18.2	
Fall						
1979	112	*	*	1.7**	0.6**	0.2**
1983	112	73.2	6.2	5.8	22.3	1.8
1984	110	228.2	2.4	5.3	18.3	1.1
1985	132	243.6	2.1	6.1	8.0	23.4
1986	119	143.0	9.3	4.0	19.2	36.8
Mean	117	172.0	5.0	4.6	13.7	12.7

* Shells and boxes not counted
** Areas 2, 4, and 5 only

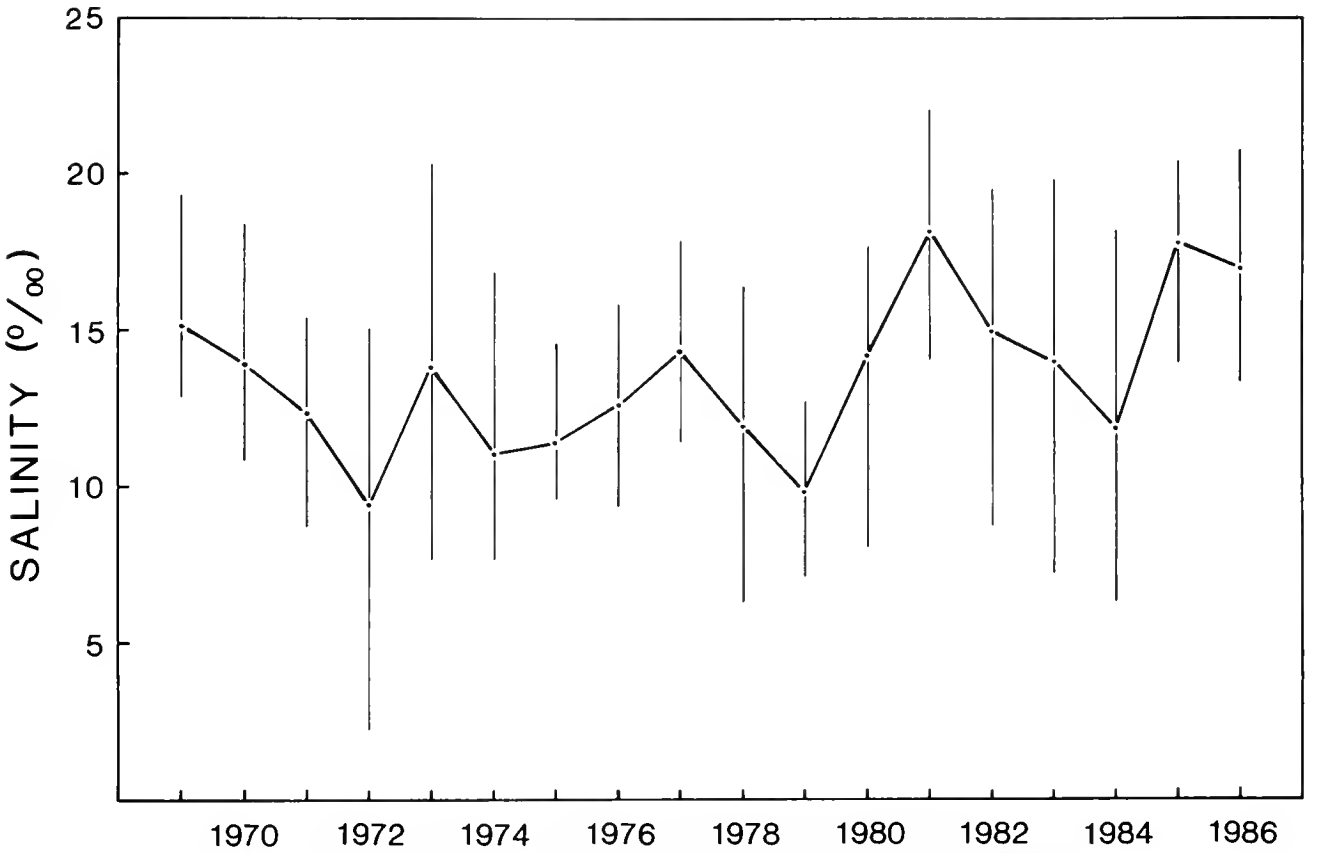

Figure 3. Annual salinity means and ranges from 1969 to 1986 near Calvert Cliffs, Maryland.

legal density was 2.3 m^{-2} and mean sublegal density was 6.0 m^{-2}.

Spat densities were similar in Areas 4 and 5 (18.2 and 18.4 m^{-2}, respectively), and lower in Area 2 (9.0 m^{-2} (Table 2). Spat density was much lower in Area 6 (1.4 m^{-2}, only 8% of the densities in Areas 4 and 5 and 16% of the density in Area 2. Although spat density was much lower in Area 6 than in Areas 4 and 5, the ratio of spat per shell was not. Combining 1985 and 1986 data revealed 0.16, 0.13, and 0.11 spat per shell in Areas 4, 5, and 6, respectively.

Oysters counted as spat in the fall were considered sublegals the following spring and eventually became legal (if they survived), yet the sublegal density was only half the spat density in Area 2, about equal to spat density in Area 4, and twice the spat density in Area 5. The sublegal density of Area 6 was 3.5 times spat density. The low ratio of sublegals to spat in Area 2 compared to the high ratio in Area 6 indicates poorer survival of spat in Area 2 (discharge area of CCNPP) than in an undisturbed area.

The ratio of legal oysters to sublegals was only 0.13 in Area 5, but was 0.31 and 0.38 in Areas 4 and 2, respectively. In Area 6, where sublegals were less abundant and harvesting was minimal, the ratio was 1.0.

Data analysis revealed no significant differences among areas in 1983 (Table 3a), but in the fall of 1984, the density of sublegal oysters in Area 5 was significantly greater ($p < 0.01$) than in Areas 2 or 6 (Tables 3a and 3b). In spring 1985, shell densities were greater in Areas 2 and 5 than in Area 6, but legal oyster densities were greater in Areas 4 and 6 than in Area 2 (Table 3b). In the fall of 1985, the spat

TABLE 2.

Mean density of legal, sublegal, and spat oysters per m^2 in four areas of Flag Pond bar for 5 years. Area 6 mean is for 1983–1986 only.

	Legal	Sublegal	Spat	Total
Area 2				
Spring	1.8	7.2	—	9.0
Fall	2.8	4.7	9.0	16.5
Mean	2.3	6.0		
Area 4				
Spring	5.2	22.1	—	27.2
Fall	5.6	12.7	18.2	36.6
Mean	5.4	17.4		
Area 5				
Spring	4.1	36.1	—	40.2
Fall	5.1	32.5	18.4	56.0
Mean	4.6	34.3		
Area 6				
Spring	4.6	5.2	—	9.7
Fall	4.8	4.2	1.4	10.3
Mean	4.7	4.7		

TABLE 3a.

Summary of F values testing the ratios of area variances to location variances from an analysis of the four areas of Flag Pond bar.

	df	Shells	Boxes	Legal Oysters	Sublegal Oysters	Spat
1983						
Spring	3/49	1.55	1.48	0.77	0.34	—
Fall	3/52	2.65	1.93	1.48	0.33	0.33
1984						
Spring	3/51	1.26	1.01	3.22	2.31	—
Fall	3/51	1.72	0.75	1.35	4.42**	2.58
1985						
Spring	3/87	4.58**	0.36	4.39**	2.69	—
Fall	3/62	3.15	2.07	0.74	2.34	4.42**
1986						
Spring	3/71	4.94**	0.87	3.95	3.58	—
Fall	3/56	1.60	3.39	2.81	2.04	3.36

** F statistic significant at $p \leq 0.01$

density in Area 6 was significantly less than elsewhere (Table 3b). Only shells differed among areas in the spring of 1986, with the density in Area 5 significantly greater than in Areas 4 or 6 (Table 3b). Densities in Table 3b were computed using means of log values, and thus differ somewhat from the arithmetic means in Table 1. Although differences among areas were few, differences among various locations and positions were common.

DISCUSSION

Shell densities were unknown prior to shell planting in 1980 and 1982 since shells were not counted in 1979, but they were probably similar to the mean densities in Area 6 from 1983 to 1986 (19.4 m^{-2}) because no shells were ever planted there. During 1983 and early 1984, overall shell densities were 60–80 m^{-2} (Table 1), but more shell planting in June 1984 increased the density nearly threefold. Although larvae set wherever they could find hard surfaces (shells, rocks, or oysters), most set where shell had been planted at densities of 1000 m^{-2} or more. In 1983, densities of sublegal oysters up to 600–800 m^{-2} were found on shell planted in 1982. Adjacent to the planted areas sublegal densities were only 5–20 m^{-2} or less.

TABLE 3b.

Results of Student-Newman-Keuls tests applied to significant differences in Table 3a. Densities are per m^2, and areas not significantly different are connected.

1984 (Fall)	Area 5	Area 4	Area 2	Area 6
Sublegal oysters	59.6	11.5	3.9	3.2
1985 (Spring)	Area 2	Area 5	Area 4	Area 6
Shells	43.8	43.6	18.8	7.1
	Area 6	Area 4	Area 5	Area 2
Legal oysters	4.0	3.1	2.1	1.0
1985 (Fall)	Area 4	Area 2	Area 5	Area 6
Spat	13.0	10.2	6.9	1.6
1986 (Spring)	Area 5	Area 2	Area 4	Area 6
Shells	79.0	27.4	17.5	11.5

The shell planted in 1984 (Fig. 2) caught very few spat that year, but salinity was low (Fig. 3), and recruitment was poor throughout much of the Bay. In 1985 and 1986 mean salinity was above 17‰, and oyster recruitment was similar to that of the early 1980s. There is little doubt about the correlation between salinity and recruitment as suggested by Ulanowicz et al. (1980), but whether increased recruitment was solely because of higher salinity or because of other factors associated with lack of rainfall, such as reduced runoff carrying pollutants into the Bay, is unclear. It is clear, however, that salinities were lower in the mid Bay during the 1970s (mean 12.0‰) than they were from 1980 to 1986 (mean 15.4‰; Fig. 3). Three excellent recruitment years occurred in 1981, 1985, and 1986 when salinity ranged from at least 13‰ to over 20‰, and averaged above 17‰ (Fig. 3). Overall mean spat densities in Areas 2, 4, and 5 were 15, 43, and 25 m^{-2}, respectively, in 1985 and 28, 43, and 62 m^{-2}, respectively, in 1986. These means, however, included samples from shell-planted bottom as well as barren bottom. Sample densities on planted shell alone were as high as 277 m^{-2} in 1985 and 510 m^{-2} in 1986. Spat in Area 6, where shell was never planted, were 2 and 3 m^{-2} in 1985 and 1986, respectively. Had cultch been planted in Area 6, it too might have had spat densities of 15–60 m^{-2} instead of only 2–3 m^{-2}.

Earlier studies (Beaven, 1948; Engle, 1956) indicated that more larvae set on newly planted shell than on old shell, and Shaw (1967) recommended planting shell in Broad Creek, Maryland during the first week of July to serve as cultch for larvae that would begin setting soon thereafter. These studies imply that cultch should be planted as close to the time of larval setting as possible, so that setting is not impeded by fouled cultch. This is still a wise management practice, as far as it is practical to do so. Yet in 1984, the newly planted shell on Flag Pond caught very few spat because few larvae were available to set. In October 1985 and 1986, mean densities of 10- to 25-mm spat on this 1984 shell were 172 and 260 m^{-2}, respectively; and the highest sample density in 1986 (510 m^{-2}) was on cultch planted in 1982. These high densities indicate that planted shell can still be highly valuable as cultch even after 4 years.

Although additional cultch will improve recruitment in some areas, it will not do so everywhere. It will not guarantee good setting in historically poor recruitment areas such as the Patuxent River in Maryland (Sieling, 1950; Kennedy and Breisch, 1981). Nor will it improve setting where the density of brood stock is inadequate to supply enough larvae (Andrews, 1983; Haven and Fritz, 1985).

Planted shell was obviously critical to increased recruitment on Flag Pond, but shells were planted too heavily in some locations resulting in loss of oysters from sedimentation and biodeposition. Where shell was spread in a layer 30 cm or more thick in 1982, larvae set throughout the entire mass. In 1983 the densities of 30- to 60-mm oysters in this mass were 400–800 m^{-2}. By 1984 these densities were reduced to 50–60 m^{-2}, all confined to the upper cultch layer; oysters below these had been smothered by sediments and biodeposits. Haven et al. (1981) indicated increased sedimentation in the James River in Virginia over the last three decades and suggested it could have affected recruitment. Biodeposition, however, can pose an even greater threat than sedimentation. Haven and Morales-Alamo (1966) determined that oysters deposited filtered material seven times faster than it settled by gravity. Lund (1957) calculated that oysters covering a hectare of bottom could produce 18.7 metric tons (dry weight) of fecal material in 11 days. Once this material settles into the crevices of a thick shell layer it is difficult for currents to remove. Thus it builds up and eventually smothers the oysters below the surface layer. Thinner layers of shell planted over larger areas may reduce mortalities from smothering and result in larger harvestable populations.

The density of legal oysters on Flag Pond bar peaked in fall 1985 at 6.1 m^{-2}, and declined only slightly to 5.8 m^{-2} in spring 1986, despite heavy fishing pressure by oystermen. By fall 1986, legal density could have reached the highest level during this study as large numbers of oysters recruited in 1981 and 1982 became legal. Unfortunately, the high salinity which allowed the exceellent recruitment in 1985 and 1986 may also have allowed "MSX" caused by *Haplosporidium nelsoni* or "Dermo" caused by *Perkinsus marinus* to invade and kill large numbers of oysters. Dredging in Areas 2, 4, and 5 from August to October 1986, as part of another study, indicated two or more boxes for each live legal oyster, and the present data (Table 1) confirm this ratio (2.3:1). Small oysters seemed less affected. Newly set spat and oysters less than 2 years old appear less susceptible to infection from Dermo than older oysters (Andrews and Hewatt, 1957; Andrews, 1966), but MSX may infect and kill all sizes (A. Farley, NMFS, Oxford, Maryland, pers. comm.).

Ratios of legal to sublegal density in the four areas reflected commercial activity. These ratios were low in Areas 2, 4, and 5 where oysters were removed from the population as they became legal. Little harvesting occurred in the rocky shallows of Area 6 which allowed legal oysters to reach higher densities relative to small oysters than elsewhere.

Based on total densities determined by summing legals, sublegals, and spat (Table 2), Area 5 has the best commercial potential of all four areas. Area 4's potential is lower, but its immediate prospects are best with a legal density of 5.4 m^{-2}. The potential of Area 2 is third best, but its immediate prospects are less than those of Area 6, which has the poorest commercial potential of all (because of low sublegal and spat densities). The low overall density of Area 6 may be unimportant from a commercial viewpoint, however, since it is a small area, and little activity occurs there; but because the legal density is similar to that of Areas 4 and 5, the oysters could be an important source of reproductive material for other areas.

Spat were scarce at all locations in 1979, a condition perhaps similar to that occurring during much of the 1970s; however, larval recruitment was vastly improved in the early 1980s. Evidence of this improvement comes from the surveys of Krantz et al. (1982), Krantz and Davis (1983), and from the increase in sublegal oysters observed in this study from 1979 to 1983. Low spat densities of only 1.8 and 1.1 m^{-2} occurred in the wet years of 1983 and 1984 (Fig. 3), but the dry years of 1985 and 1986 resulted in spat densities of 23.4 and 36.8 m^{-2}, respectively. The outlook for this area of the Bay is better now than at any time in the past two decades, provided that disease mortality is not too great.

The statistical differences common among locations and between positions probably resulted because of patchy distribution of oysters within larger areas. Even when areal densities were similar, some locations supported large component densities while others supported low densities or were barren. Patchy distribution of spat is typical on bottom consisting of scattered rocks and shells, because larvae are limited by where they can set. Even where favorable substratum exists, e.g., where shells have been planted, oysters may set gregariously as suggested by Crisp (1967). Hidu (1969) demonstrated in lab experiments that the presence of spat on cultch attracts more larvae and stimulates setting.

The oyster population of Flag Pond bar was estimated to be 7×10^3 bu in 1979 based on 200 legal oysters or 400 sublegals per bushel (spat were not included in the estimate). By 1983, the population estimate had increased to 54×10^3 bu. Although population size decreased during 1984–85 because of natural mortality and heavy pressure from commercial harvesting, the population was estimated at 43×10^3 bu in 1986, more than six times greater than in 1979.

With overall sublegal densities more than 18 m^{-2} in 1986 and spat at nearly 37 m^{-2}, the prospects for increased harvests from Flag Pond bar over the next few years are good, provided lower (normal) salinities reduce the suspected disease problem. Flag Pond is not unlike many other oyster bars in central Chesapeake Bay, and if similar recruitment has occurred on them over the past 2 years, Maryland oyster harvests should begin to improve from the poor season of 1986–87 with increased catches for the next few years.

A comparison of Areas 4 and 5 with Area 6 may best illustrate the value of shell planting, even after several

years. Portions of Areas 4 and 5 were planted with shell in 1982 and 1984; Area 6 received no shell. The mean sublegal density in Areas 4 and 5 was 25.8 m^{-2}; the mean sublegal density in Area 6 was 4.7 m^{-2}. The mean spat density in Areas 4 and 5 was 18.3 m^{-2}, Area 6 had 1.4 spat m^{-2}. These differences in oyster density between planted and unplanted areas are considerable and result from the availability and absence, respectively, of suitable substratum on which larvae can set. The number of larvae that can set is proportional to the area of clean shell surface (MacKenzie, 1983). Numbers of spat per shell were much more similar among these areas than spat densities.

During years of low larval recruitment, shell planting at first appears to waste resources, but recruitment success is difficult if not impossible to predetermine. If planting is conducted annually, recruitment during some years will surely be inadequate to increase population, e.g., most of the 1970s. Shell planting during poor reproductive years, however, can still be a valuable practice as shown by the high spat densities of samples in 1986 from 4-year-old planted shell. Planted shell may be of little value, however, if buried by shifting bottom or spread in water deeper than 9 m which may become anoxic in summer (Taft et al., 1980; Officer et al., 1984), but when put down prior to above average recruitment, it can result in much greater oyster densities than would otherwise occur. Shell planting therefore continues to be a major means to increase oyster production in Maryland.

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THE APPLICATION OF HYDROACOUSTICS TO THE MAPPING OF SUBTIDAL OYSTER REEFS

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ABSTRACT Hydroacoustic techniques were used to delineate the extent of subtidal oyster reefs in the three tributaries of Chesapeake Bay. The instruments included a precision survey echo sounder operating at 200 kHz, and a side scan sonar system operating at 100 kHz. The sounder proved to be a useful and economical tool to remote sense bottom type and topographic features along a narrow path (<2 m) across the estuary. The sonar mapped a considerably wider swath (200 m) along vessel track, providing 100 percent coverage of the bottom when adjacent echograms were mosaicked. The sonar did not provide additional capability in identifying bottom type or resolving types of oyster reefs, but produced data that was used to assess sedimentary processes and environmental impacts to the oyster reefs. In this regard, bottom scars with a total extent of almost 20 km were observed on Wreck Shoal in the sonar records. These are attributed to the passage of commercial vessels over the shallow oyster reef.

KEY WORDS: Hydroacoustic mapping, oyster reefs

INTRODUCTION

High frequency hydroacoustic instruments (20–200 kHz) have been used to delineate and estimate the abundance of finfish resources since the 1950's (Johannesson and Mitson 1983, Thorne 1983). Low frequency hydroacoustic techniques (3–10 kHz) have been utilized to investigate the subbottom character of the oyster reefs in Texas (Bouma 1976) and Virginia (DeAlteris 1987). The published literature is devoid of an evaluation of the application of high frequency hydroacoustics to the mapping of subtidal oyster reefs. Galtsoff (1964) described an oyster reef as an aggregation of live oysters and empty shells occupying the bottom of an estuary. An oyster reef is further defined herein to include estuarine bottoms consisting of live oysters and shells with densities of live oysters from sparse and scattered (10/m^2) to very concentrated (1000/m^2).

The purpose of the hydroacoustic surveys described in the sequel was to: 1. delineate the limits of the subtidal oyster reefs from the adjacent bottom, 2. investigate in detail any bottom topographic features and textural patterns that might provide insight into the estuarine sedimentation processes operating on the oyster reefs, and 3. identify evidence of damage to the oyster reefs that might be associated with commercial activities on the estuary such as dredging or transportation.

In coastal and estuarine waters, oystermen and researchers have used a variety of techniques to detect subtidal oyster reefs. Moore (1910) used a chain attached to a cable and dragged over the bottom to identify the character of the bottom in the James River, Virginia. When passing over an oyster reef, the vibrations of the chain dragging over shells were transmitted up the cable to the operator tending the gear. Tongs were used to periodically sample the bottom, ground truthing the results of the remote sensing technique. This technique is still used by oystermen searching for uncharted oyster reefs to harvest. The public oyster reefs of the Virginia portion of Chesapeake Bay and its tributaries were mapped during the 1970's using an electronic version of Moore's technique (Haven et al. 1979, Haven and Whitcomb 1983). The presence or absence of shells and/or oysters was monitored continuously with an underwater microphone mounted in a steel frame and dragged from a cable behind the vessel. The sounds made by the microphone bouncing over shells and oyster or sliding over sand and mud were amplified and broadcasted. The intensity and frequency of the sounds and the percentage of time the microphone was impacting on shells or oysters or other bottom types were recorded by the operators. These data were periodically compared to ground truth samples taken with tongs.

Data collected from oyster reefs in three tributaries of the Chesapeake Bay are used to evaluate the effectiveness of two hydroacoustic mapping techniques.

Wreck Shoal is a subtidal oyster reef located in the James River estuary, Virginia. The James River is a major tributary of the southern portion of the Chesapeake Bay. The estuary is approximately 80 km long and varies in width from 3 to 10 km. Channel depths range from 6 to 28 m. The Wreck Shoal study area is in the middle of the James River estuary with water depths ranging from 3 to 9 m, and encompasses an area of approximately 8 km^2. Two significantly different types of oyster reefs are found in adjacent areas of Wreck Shoal study area. The hard-rock reefs are characterized by a relatively thick shell layer (>2 m), higher densities of live oysters (91/m^2), a coarser interstitial sediment (37% gravel, 40% sand, 23% silt-clay) and a negligible sediment cover. In contrast, the mud-shell reefs are characterized by a very thin oyster shell layer (<10 cm), considerably lower densities of live oysters (28/m^2), a finer interstitial sediment (8% gravel, 25% sand, 67% silt-clay), and a 1–2 cm layer of very fine sediments covering the reef. The hard-rock reefs are flourishing with respect to

oyster productivity and shell deposition, and are non-accretional with respect to fine sediments. The mud-shell reefs are marginal in oyster productivity and shell deposition, and are accretional with respect to fine sediments (DeAlteris 1986).

The Back River is a small, shallow tributary of lower Chesapeake Bay, 9 km in length, with a mean depth of 2 m. The axis of the main channel bifurcates into the Northwest and Southwest Branches of the Back River at approximately the midpoint along its length. The Back River study area included oyster leases in both branches of the estuary. The mouth of the Back River is located 10 km north of the mouth of the James River. In contrast to the large, public domain natural oyster reefs of the James River, the bottom of the Back River has been divided into private lease areas for the cultivation of oysters. The productivity of these areas is dependent upon the investment made by the leaseholder in shell stock and seed oysters. The natural bottom in the major portion of the Back River is a soft mud. Areas that are actively cultivated have thick shell layers (10–20 cm) and oyster densities of 10–50/m^2 distributed over several hectares.

The Wicomico River is a narrow meandering tributary of the upper Chesapeake Bay, Maryland, and is more than 30 km in length. Oysters are produced on both public and private bottom in this estuary. The mouth of the estuary is relatively wide (2.5 km) and shallow (2 m). The Wicomico River study area included two lease areas and was approximately 3 km upstream from the mouth of the estuary, with water depths of 2–3 m.

MATERIALS AND METHODS

Two acoustic methods are evaluated as to their ability to distinguish the bottom hardness and roughness and the topographic features associated with an oyster reef. Both instruments operate at relatively high frequencies.

The conventional method was echo sounder, which employs a vertical axis acoustic beam. A Raytheon DE-719B precision survey fathometer operating at 200 kHz was utilized. The transducer employed 10 deg beam width directed toward the bottom. In shallow water, the strength of the reflection is determined principally by the reflectivity of the target (target strength), in this case the bottom. In less than 10 m of water, the width of the swath of bottom coverage is less than 2 m. Multiple reflections may appear on the echogram depending on the gain setting of the receiver-amplifier. By setting the gain so as not to produce a second reflection on a soft, non-reflective bottom, when the sounder passes over a harder, rougher bottom with a higher target strength, a second reflection appears on the echogram. Thus, by tuning or effectively adjusting the gain setting of a sounder, the instrument can be used to easily distinguish between the hard, rough bottom of an oyster reef and a soft mud bottom.

The other method, a side scan sonar, used an acoustic beam with its main axis slightly below horizontal. The beam is very narrow in the horizontal plane, yet sufficiently broad in the vertical plane to obtain echoes from a point on the bottom directly below the transducer to points 100–200 m abeam of the transducer. The combination of the beam shape and the very short length pulse length gives the sonar the capability to resolve small topographic irregularities and differences in roughness in the sea floor. As the transducer is towed below the survey vessel, the reflected or backscattered echoes are graphically recorded in a form that approaches a topographic or plan view map. Projections above the bottom and acoustically rough surfaces are good acoustic backscatters, and therefore darken the sonogram. Depressions of the bottom or relatively smooth bottoms are represented by a lightening of the sonogram. A Klien Hydroscan System was used, operating with 100 kHz transducer frequency at the 100 m range, and displaying on a dual channel, analog, wet-paper recorder.

Navigation control for the Wreck Shoal acoustic surveys was provided by LORAN C, using a Northstar 7000 system. The navigation unit was point calibrated at a known location at the beginning and end of each survey day. Fix marks were noted every 100 m along each transect. Navigational accuracy was approximately ± 20 m, or ± 0.1 micro-second of time difference in LORAN C signals. Position determination in the Wicomico River and Back River acoustic surveys was accomplished using visual ranges to shore mounted monuments.

The Wreck Shoal study area was 4 km long by 2 km wide. The track lines for the Klien sonar and the precision bathymetry survey were spaced 91 m apart. The Klien sonar was operated at the 100 m range, which resulted in approximately a 50 percent overlap in the records. The Back River study area included almost the entire estuary and transect lines for the echosounder were spaced so as to bisect individual lease areas for the identification of actively cultivated areas, that could be further investigated with conventional sampling techniques. The Wicomico River study area was limited to two private lease areas near the mouth of the river. Three acoustic survey transect lines were run with the echo sounder over each oyster ground to identify the patch oyster reefs and to search for evidence of an alledged grounding by a large commercial vessel.

The Wreck Shoal surveys were conducted in June, July 1984, and March 1985. The Back River survey was conducted in May 1981, and the Wicomico River survey was conducted in April 1985.

RESULTS

The hydroacoustic survey of the Back River included more than 25 private lease areas, only two of which are discussed herein. In the transect across the N.W. Branch of the Back River (Figure 1, upper echogram), the echo sounder began in the nearshore area at Langley A.F.B., crossed the channel with a maximum depth of 2.4 m, and

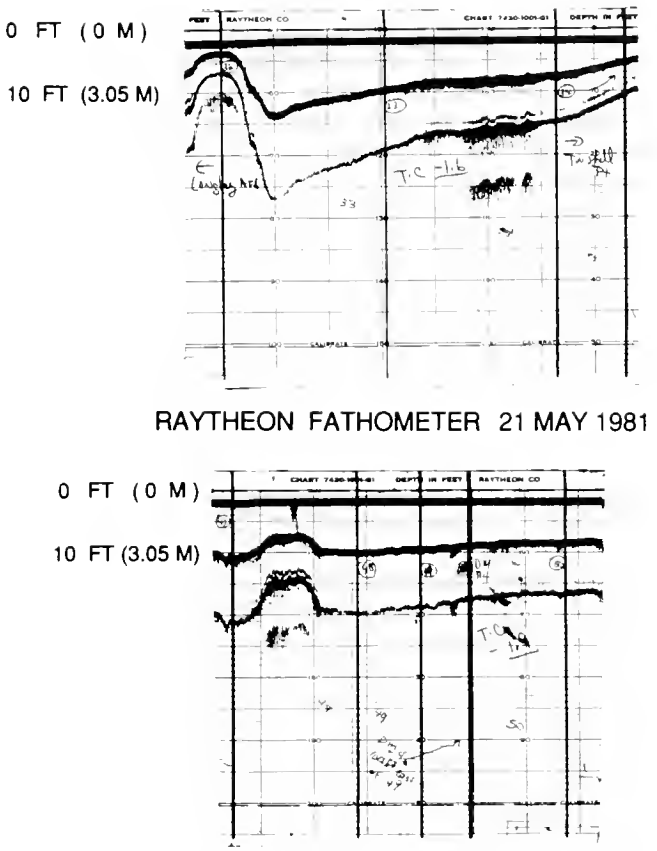

Figure 1. Echograms from the Back River, Virginia, showing transects across lease tracts in each branch of the estuary.

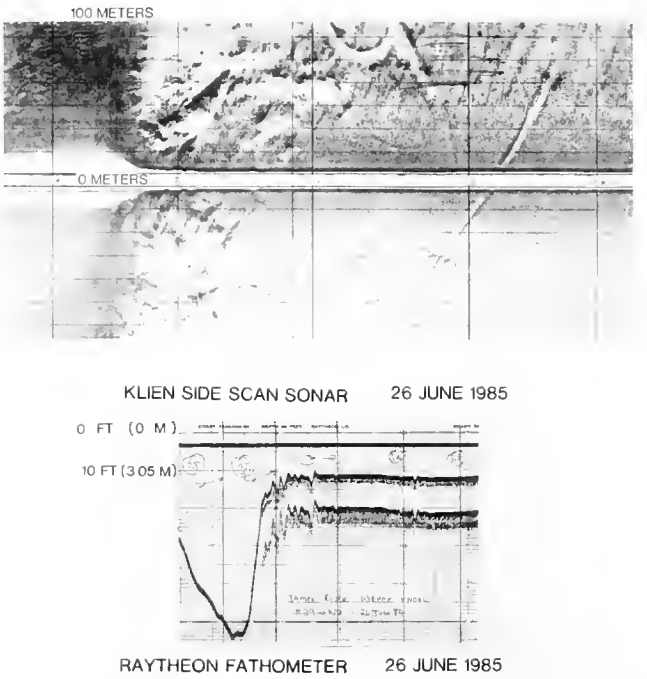

Figure 2. Echogram and sonogram from Subarea B, Wreck Shoal, James River, Virginia, showing the channel axis, the north bank of the channel, and the shallow hard-rock oyster reef. The fix marks 3.8 to 3.4 were made at 100 m intervals.

reached the opposite shore of Tin Shell Point. The bottom type between fix marks 32 and 33 was a soft mud and between fix marks 33 and 34 graded into and out of hard-shelled oyster reef. The location of this oyster reef was indicated by the presence of the second and third reflections in the echogram, and was confirmed by tong sampling. The mean density of oysters on this reef was 43/m^2. This was a planted oyster reef, and was not perceptable above the natural bottom elevation. During the transect across the S.W. Branch of the Back River (Figure 1, lower echogram), the echo sounder passed over large topographic high, with second and third reflections evident in the echogram. Sampling with tongs confirmed the identification of an oyster reef with a density of 65/m^2.

An extensive hydroacoustic survey of the Wreck Shoal study area was conducted using both an echo sounder and side scan sonar simultaneously. Two subareas were selected for detailed analysis and comparison of the results of the sounder and sonar surveys.

Subarea B is located along the flank of the natural channel on the inshore portion of the study area. The precision bathymetry along the center line of the area and the original record of the Klien side scan sonar are shown in Figure 2. Fix mark 3.8 denotes the center of the main channel, with step rising bank to fix mark 3.7. The channel bank rises from 15.3 to 6.1 m in a 30 m distance or about 10 m to 30 m, for a slope of about 20 deg. Along the edge of the bank, there are a series of features of nearly uniform wavelength of 10 m and a height of 0.3 to 0.9 m. From fix mark 3.7 and beyond, there is a strong second reflection in the echo sounder record, indicating a hard, rough bottom. Ground truth data collected with oyster tongs in this area confirms the presence of a dense oyster reef (91/m^2). On the shallow hard oyster reef portion of the study area, beyond fix mark 3.5, a bottom scar 0.3 m in depth passes the center of the sonogram. There is another distinct scar visible in the upper part of the sonogram. Subsequent surveys of the area in July 1984 and March 1985 with an E.G. & G. side scan sonar reveal identical features on the bottom.

Subarea C is located in the central portion of the Wreck Shoal study area, in the relatively deep trough zone that makes up the mud-shell oyster reef environment. Water depths range from 4.0 to 5.5 m. The echogram suggests two different bottom types in subarea C (Figure 3). From fix marks 2.0 to 1.8, the presence of a weak second reflection indicates a mud-shell oyster reef. In contrast, from fix-marks 1.7 to 1.4, the absence of a second reflection indicates a soft mud bottom type. Ground truth data collected with oyster tongs confirmed a mud-shell oyster reef (oyster density of 28/m^2) in the downstream portion of the area and a soft mud bottom with very scattered shells and oysters (oyster density of 4/m^2) in the upstream portion of the area.

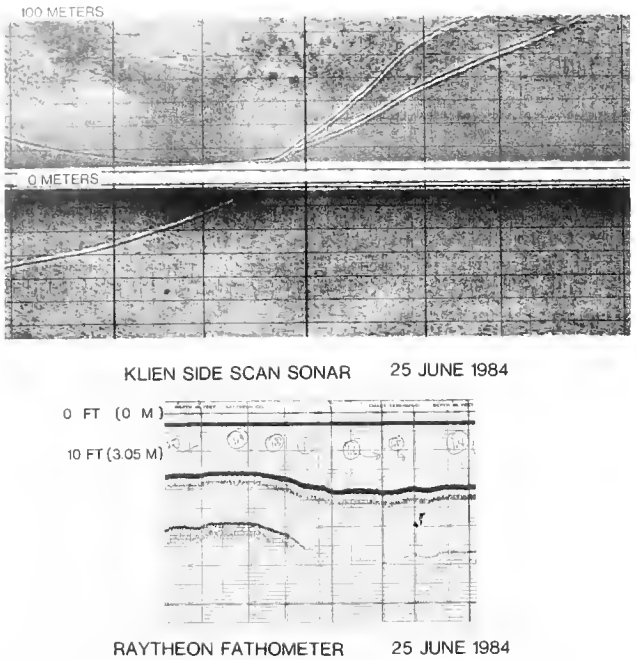

Figure 3. Echogram and sonogram from Subarea C, Wreck Shoal, James River, Virginia, showing a transition zone between a mud-shell oyster reef and a mud bottom. The fix marks 2.0 to 1.4 were made at 100 m intervals.

Unfortunately, it is impossible to distinguish between the mud-shell reef and the mud bottom in the sonar record. The sonogram does show two segments of a continuous bottom scar that passes beyond this record, turns around, and passes back over this record. When adjacent sonograms were mosaicked, the length of this bottom scar was greater than 2 km. The center line of this transect passes over the scar between fix marks 1.8 and 1.7, and the record indicates the depth of the scar is 0.2 m. Subsequent surveys of the area of July 1984 and March 1985 with an E. G. & G. side scan sonar indicate identical features on the bottom, but again there was no distinction between bottom types.

Six transects from the Wicomico River were taken on two private lease areas. A large commercial vessel with a draft of 2.9 m had allegedly run aground in the lease areas and caused damage to the oyster reef. The echosounder survey data of this area was corrected for tide elevation on the instrument, and therefore indicated depths relative to high water, to coincide with the tide elevation at the time of the alleged grounding. The echogram (Figure 4) indicates water depths in the lease area range from 1.8 to 2.9 m at high water, precluding the possibility of grounding a vessel on all but the outer edge of the lease area. The record also indicates that bottom type varies from hard oyster reef to a mud bottom. Tong sampling on the larger offshore oyster reef indicated an oyster density of 118/m^2. Diver inspection of the bottom also confirmed a lack of recent sediment deposits on the oyster reef that would suggest a vessel had grounded and then attempted to power-off from that area.

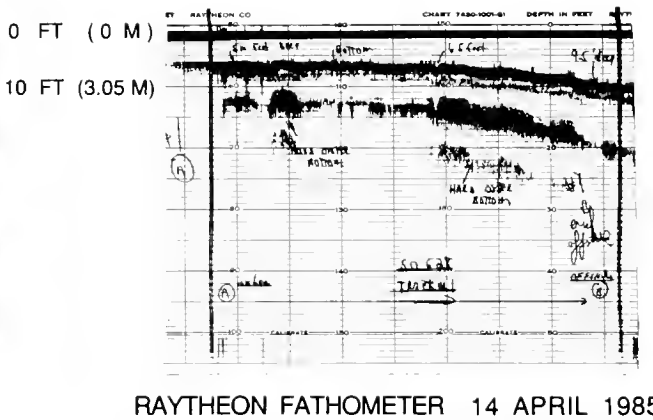

Figure 4. Echogram from the Wicomico River, Maryland, showing a transect across a lease tract.

DISCUSSION

Based on the results presented previously it is clear that an echo sounder is capable of delimiting subtidal oyster reefs from the adjacent estuarine bottom. Depending on the type of the reef, the echogram may indicate the reef as a topographic high relative to the adjacent bottom. However, the definitive test for identification of the reef is the presence of second and third reflections in echogram of a properly tuned echo sounder. Recall that proper tuning is the reduction of the gain in the receiver-amplifier so as to produce only a single reflection on the echogram from a mud bottom. In addition, it appears that an echo sounder is capable of discerning between types of oyster reefs, such as the hard-rock and mud-shell types. However, the distinction is much more subjective than a simple presence or absence test. The interpretation of the side scan sonar record is not as clear as the echo sounder. Under some circumstances (data not presented here), the sonar has demonstrated the capability of distinguishing between mud bottoms and oyster reefs. Yet, in other cases, as in the Wreck Shoal study area, the interpretation is not as clear. In fact, it is impossible to delineate between either the presence or absence of an oyster reef or between types of oyster reefs in these data.

The secondary objective of the hydroacoustic surveys was to identify any textures or patterns on the bottom of the study areas that might assist in assessing the sedimentation processes operating in the areas. In that regard, the results of both the echo sounder and sonar surveys are most useful. Both instruments reveal scars in the bottom when present.

There are several possible explanations for the scars on Wreck Shoal. Perhaps the most plausible would be an anchor or dredge dragging across the bottom, or possibly the keel of a boat. The width of the tracks or scars (5–10 m) was directly measured from the side scan sonar record. The precision echo sounder records the vertical dimension of the scars when they pass directly under the survey vessel. The depth of the track varies from 0.1 to 0.9 m. Water

depths in the areas of the scars range from 2.7 to 5.5 m. Because of the width and depth of the bottom scars and the water depth, it is doubtful that any of the above explanations reasonably account for these marks. An alternative explanation is that the marks have been caused by the propeller wash of large commercial vessels operating out of the navigation channel, crossing Wreck Shoals.

Following a methodology developed by Liou and Herbich (1976), it can be shown that shallow draft commercial vessels in the James River are capable of generating propeller wash exit velocities in excess of 10 m/sec. This jet of water moving downstream from the propeller would generate maximum bottom velocities of 10.7, 3.4 and 2.0 m/sec in water depths of 3.1, 4.3, and 5.5 m, respectively. These water flows are certainly capable of scouring the bottom and creating the wide trench observed on both the echograms and sonograms. It is the longevity of these scars on the bottom that is of interest, with respect to sediment transport processes on Wreck Shoal. The sonar indicated no observable change in the majority of the bottom scars between two surveys, a period of nine months. This implies that there is not much active sediment transport occurring on Wreck Shoal. These trenches would have otherwise filled and become unrecognizable. Future surveys of Wreck Shoal will be able to determine exactly how long these features remain.

The sonar surveys identified about 19+ km of bottom scars with the width of the scars about 10 m including the adjacent banks. Therefore, the resulting area impacted is $2 \times 10^5 m^2$ or about 20 hectares. In terms of the total area of the Wreck Shoal study area (more than 800 hectares), the area affected by the bottom scars is less than two percent.

ACKNOWLEDGMENTS

Support for the field work in this project was provided by the Virginia Institute of Marine Science through the James River Seed Oyster Bed Project. The University of Rhode Island provided support through the Summer Faculty Fellowship Program and the College of Resource Development, Agricultural Experiment Station. This is contribution number 2390 of the University of Rhode Island, College of Resource Development, Agricultural Experiment Station, Kingston, R.I., U.S.A., 02881.

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OVERWINTERING AMERICAN OYSTER SEED BY COLD HUMID AIR STORAGE

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ABSTRACT Young-of-the-year hatchery produced American oysters were successfully humid air stored at 0° to 6°C for monthly periods up to 6 months. Survival of oysters between 6 and 55 mm length was uniformly high, over 80%, and equaled or exceeded that of seawater stored controls in nearly all cases. There is an indication that premature replacement back to ambient sea water before April was detrimental to survival. Measurement of growth and survival after the subsequent summer season revealed continued high survival, but those returned to water after April had grown less. The decreased growth rate is probably due to lack of exposure to the complete growth season. Trials with local industry indicate that air storage of juvenile oysters may be practical on a commercial scale.

KEY WORDS: Overwintering, air storage, oysters, American oysters

INTRODUCTION

In recent years shellfish hatcheries and associated field nursery operations have been prominent in North America. In Maine, American oyster seed (*Crassostrea virginica* L) is economically reared to a 25–60 mm size in its first season in floating tray fields (Clime & Hamill 1979). After the first year, however, tray deployment becomes unwieldy and uneconomic, making bottom culture the only alternative. Thus the handling of large quantities of seed oysters over the first winter has become a major problem. Holding oysters in trays in the field exposes them to silting and weather related loss. Onshore sea water systems are expensive and unreliable. Planting, especially small 25 mm clutchless seed oysters, in early winter has resulted in substantial loss due to predation by eider ducks (R. Clime personal communication). Cold humid air storage is a potentially attractive strategy for overwintering seed. Acceptable winter survival of seed would afford nursery-growout operations greater profit and the hatcheries could more efficiently expand their production season and offer yearling seed for sale the following spring.

Air storage of American oysters has received earlier attention from a marketing but not a culture perspective (Friedman, 1933, Needler, 1934; Medcof, 1960). The criteria for success with market oysters are palatability and salability. The criteria for continued culture would merely be survival and subsequent ability to grow. Anecdotal evidence (Medcof, 1960) indicates that humid cold air stored market oysters were edible, presumably alive, after 4, 6, and even 8 months of air storage. Thus the potential exists for long term storage viability. Market oysters at 34°F (/°C) showed negligible mortality at 3 months but incurred 40% mortality after 5 months. (Medcof, 1960). Mortality was higher at storage temperatures of 41–60°F at 5 months.

This study reports survival and subsequent growth of several sizes of American oyster seed overwintered in humid air up to 6 months at several temperatures. Results of scale up commercial overwintering trials are described.

Methods 1986 Experiments

Young-of-the year cultchless seed oysters produced from Maine stock were procured from ambient (Figure 1) sea water upwelling units at Mook Sea Farms, Walpole, Maine, in late December 1985. These were screen graded into two size groups ($\bar{x}$ = 7 mm S = 1.2 and ($\bar{x}$ = 9 mm; S = 1.2). Each group of oysters was subdivided into subgroups of 200 and each placed in 100 mm × 15 mm disposable plastic petrie dishes. The dishes were lined with several sheets of brown paper toweling wetted with sea water at approximately 30 salinity. Petrie dish bottoms were drilled to drain any accumulated water. Appropriate sets, (6 sets of 5 petrie dishes with no replicates) were placed in tightly sealed plastic containers, also containing damp toweling, to be periodically removed for sampling. Container sets were then placed in 3 constant temperature units at 0, 3 and 6°C (±0.5° approx.) Oysters were removed from the Petri dishes and placed in ambient sea water in mesh bags at t = 0 months (control), 1, 2, 3, and 4 months (Figure 1). After 4.6 months, the last group of oysters were removed and it and all other oysters were incubated for one month in 400 liter rearing vessels at 15°–20°C with cultured algal mixtures *Isochrysis galbana* and *Chaetocerus* sp. fed commensurate with clearance

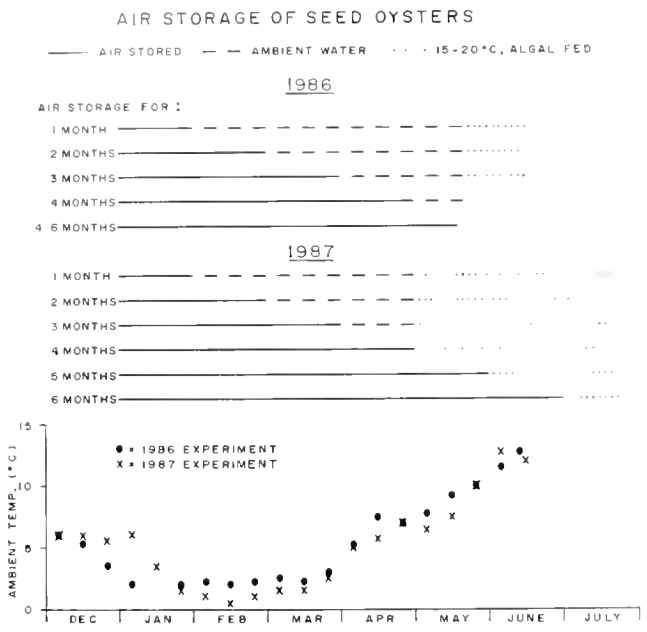

Figure 1. Experimental regimes in the humid air storage of American oyster cultchless seed in 1986 and 1987 with associated ambient seawater temperatures.

rates. Vessels were drained and cleaned three times per week.

After the incubation period, determinations of living and dead oysters were made under a dissecting microscope. Three categories were evident: dead (shells permanently agape), live (new shell growth); and "presumably live" (shells tightly closed but no shell growth). To determine viability of the "presumably live" animals, a single group (9 mm held at 3° for all time periods) was held an additional month in warmed sea water and fed as above. The additional month allowed the oysters to either add new shell or die. With differential survival subsequently shown in the different monthly groups, it would have been highly desirable to incubate all oysters for an additional month. However, this limited information helped us with the design of the second year confirmatory results.

1987 Experiments

The second year trials were modified in accordance with first year's experience (Figure 1). These experiments included two groups of young of the year seed oysters, 12 mm (S = 1.4) and 40 mm (S = 5.0) and were humid air stored at 0°C with a second group of the 12 mm oysters air stored in a home refrigerator at 4 to 6°C as insurance against equipment failure. Oysters after 0–3 months air storage were placed directly in ambient sea water before the warm water incubation period (Figure 1). Oysters stored for 4 to 6 months were placed directly in warmed algal fed baths as above. The warm sea water-algal fed incubation period was lengthened to 1.5 months minimum to allow determinations of viable oysters. A failure of the 0° cold unit on May 15 at 4.5 months prompted us to remove all 5 month groups to ambient sea water 15 days early and to place the 6 month groups in air storage at 4–6°C for the remaining 1.5 months of storage. The failed unit registered 16°C and may have been at that temperature up to 3 days before discovery.

All of the 40 mm group were then held over the remainder of the summer in field nursery lantern nets to determine the effects of the treatments on subsequent growth and longer term viability of the living oysters. Mean lengths and total wet weights with standard errors of the mean (±) 2 S_{EM}) of this group were determined on September 30, 1987.

RESULTS

1986 Experiments

Initial determinations of viability after 1 month of incubation under optimal conditions revealed a high "apparent" survival of the 7 and 9 mm oysters regardless of length and temperature of air storage (Figure 2). Lack of replication within treatments did not permit statistical analysis but it is apparent that survival in the 7 mm oysters was 5 to 10% poorer than the 9 mm oysters. The anomolously low survival of the 7 mm seed oysters air stored for 4 months is no doubt due to error in determining live and dead oysters.

Culture of the 9 mm 3°C "presumably live" group re-

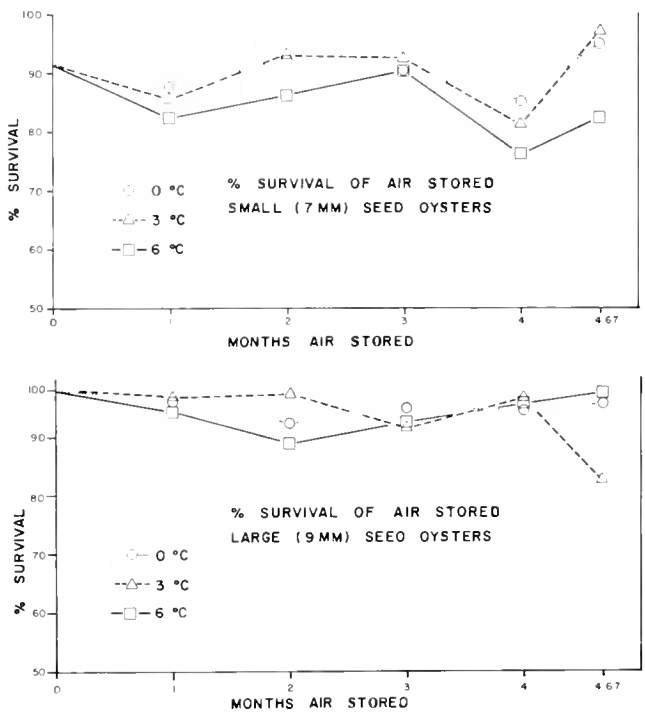

Figure 2. "Apparent" survival of 7 mm and 9 mm seed oysters after air storage up to 4.6 months in 1986. These figures are erroneously high since live oysters which did not show growth 1 month post storage suffered later mortality.

vealed an apparent relationship between the length of storage and viability (Figure 3). Those held in air storage the longest 3, 4, and 4.7 months had survivals of 70% to 95% whereas those held in air storage for 1 and 2 months had less than 65% survival. This finding prompted us to modify our experimental protocol in the second year.

1987 Experiments

Survival of seed oysters after 1 to 5 months of air storage was high, generally over 80%, and increased mortality at 6 months related to size. (Figure 4). The 40 mm oysters experienced a 95+% survival to 6 months despite the fact that the last two groups experienced a 16° temperature shock at 4.6 months. The smaller 12 mm oysters survived well but at reduced levels than the larger oysters. Temperature here, 0° vs 4–6°, had little apparent effect on survival. There is a suggestion, again, in the 0° group that an avoidance of early placement in cold ambient seawater enhances survival. Survival in the oysters removed from air storage in May and June approximated 95% whereas the controls and those removed earlier approximated 85%. Six months of air storage appears to approach the limit for the 12 mm oysters as evidenced by the reduction to 80% survival in the 4–6°C group. The drastic reduction in survival down to 25% in the 0° group of 12 mm oysters has no doubt been enhanced by the 16° temperature shock experienced at 4.5 months.

Air storage did not affect the ability of seed oysters to survive and grow through the subsequent summer season. The 40 mm seed oysters of 1987 continued to survive over 95% through the end of September. Ability to grow was not affected (Figure 5) however it is obvious that those which were air stored the longest, and thus deprived of increasing portions of the growth season, grew the least. This is apparent particularly in the September total weights of those

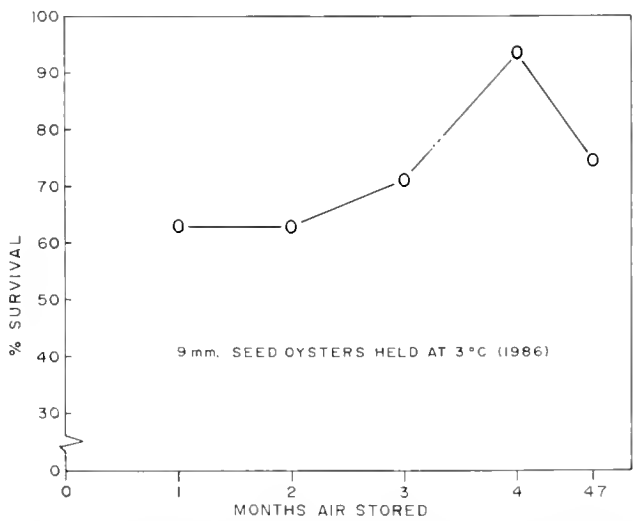

Figure 3. "Actual" survival of 9 mm seed oysters damp air held at 3°C up to 4.6 months in 1986. Oysters were held 2 months in warmed algal-laden water post storage before viability determination.

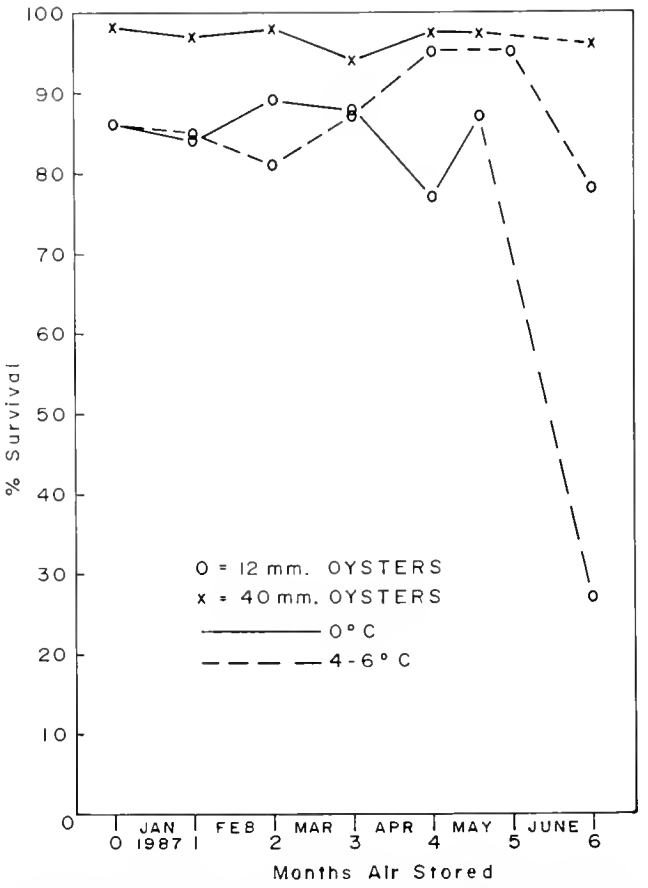

Figure 4. Survival of 12 and 40 mm seed oysters at two temperatures after up to 6 months air storage. Cold unit failure at 4.5 months in the 0°C groups necessitated premature sampling of 5 month groups and placement of 6 month groups at 4–6°C.

air stored for 4, 5 and 6 months (through April, May and June.) Shell lengths, although there was a declining trend, were not affected as drastically as weight.

DISCUSSION

The ability of seed oysters to withstand humid air conditions for a period of six months represents remarkable ability to withstand adverse conditions. The compelling questions are: what are the physiological mechanisms allowing prolonged survival and indeed how long can an oyster remain alive out of water? We tested only to 6 months in the second year because practical application of our results requires only 3–5 months storage. The first year's experiments were terminated at 4.6 months because a sample of oysters upon dissection appeared dead. The shells were tightly closed but the meats were in a highly desiccated condition. When these were immersed in sea water there was no evidence of heartbeat and the mantle tissue showed no response to probing with a needle. When the remaining intact oysters were subsequently incubated in warmed algal-laden sea water, they resumed feeding and over 80% survived in nearly all cases.

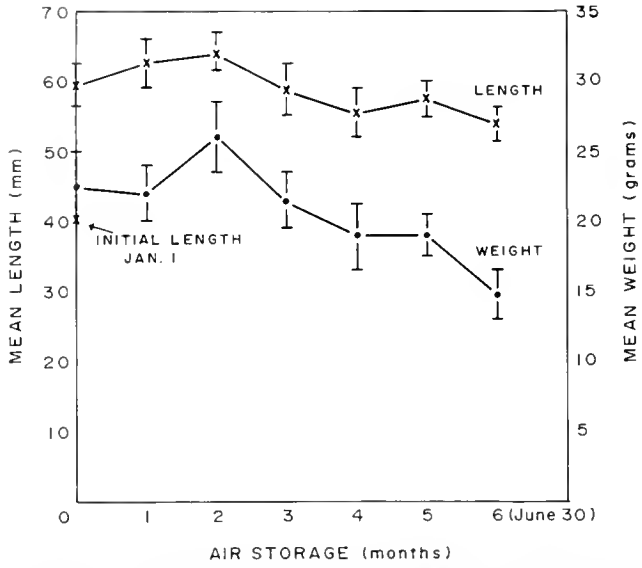

Figure 5. Shell length and total weight of 40 mm air stored seed oysters sampled September 30, 1987 after one growth season post air storage. Initial weights were not recorded. Survival in all groups exceeded 95%.

The physiological mechanisms of such survival should be investigated. Although we made no measurements of glycogen utilization, the reduced survival of those placed back in winter sea water after only 1 and 2 months air storage would suggest that glycogen utilization rates are somehow lessened with cold air storage. The air stored sample dissected in May, although again in an extremely desiccated condition, appeared to carry some remaining glycogen reserve. If glycogen utilization shuts down under cold air conditions then it might be possible to air store oysters for an indefinite period. Our follow-up studies will air store oysters up to 1 year.

Scale-up commercial application is cautiously under way in Maine. Mook Sea Farms hatchery has constructed a 4′ × 6′ × 4′ deep wood lined underground pit for over winter storage of hatchery seed. In cooperation with Dodge Cove Marine Farm, Walpole, Maine, approximately 70,000 six to ten mm and 50,000 twenty to thirty mm American oyster seed were overwintered from December 1986 to May 1987 with over 90% survival. Oysters were in 1″ plastic mesh bags in damp layered burlap and seaweed. Temperatures ranged from 1° to 10°C throughout. Other commercial trials, however, should proceed strictly on an experimental basis because of possible effects of such untested variables as physiological condition, geographical race of the stock, and variability in storage conditions such as temperature and percent humidity.

These results suggest other commercial use of air storage of shellfish as a culture technique. For example, it may be possible to avoid an infective period of a parasite by relatively short air storage periods. This might be particularly valuable with yearling oyster nursery stock in MSX, *Haplosordium nelsoni*, endemic areas. The possibilities for overwinter storage of other species, particularly hard shelled clams *Mercenaria mercenaria*, are self-evident and are under investigation. In summary, the old idea and practice of cold air storage of market oysters to prolong viability and shelflife should be investigated and expanded for its use as a culture technique as an avoidance procedure against adverse environmental components.

ACKNOWLEGMENTS

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DEVELOPMENT AND EVALUATION OF TECHNIQUES TO STUDY ACQUIRED IMMUNITY TO *PERKINSUS MARINUS* IN THE OYSTER, *CRASSOSTREA VIRGINICA* (GMELIN)

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ABSTRACT This paper describes a radiometric technique developed to measure phagocytosis of *Perkinsus marinus* zoospores by oyster hemocytes. The spores of *P. marinus* were radiolabeled by culturing *P. marinus* presporangia and sporangia in estuarine water (22‰) containing ^{14}C-glycine. The percent of spores phagocytized by hemocytes was determined by the uptake of radioactivity by hemocytes.

Results from preliminary experiments to test the efficiency of using an osmotic infiltration method for immunizing oysters are also reported. It was found that oysters can take up both dissolved antigen (radiolabeled bovine serum albumin) and particulate antigen (^{14}C-labeled zoospore homogenate) through osmotic infiltration. The uptake of the antigen was correlated with the concentration of antigen added to the water but was not affected by water temperature.

KEY WORDS: Oyster, acquired immunity, techniques.

INTRODUCTION

Perkinsus marinus (Dermo) and *Haplosporidium nelsoni* (MSX) are two parasitic pathogens which have been destructive to estuarine oyster populations in the Middle Atlantic Region since the introduction of *P. marinus* in the 1950's and MSX in the 1960's. However, there are some oysters that have survived the invasion of these pathogens (Andrews 1968; Haskin and Ford 1979; Ford and Haskin 1986). Those oysters that survive the epizootics are believed to possess certain genetic, or physiological characteristics which make them less susceptible to the pathogens (Maryland Sea Grant 1983, National Fisherman 1983). Two hypotheses have been suggested for the occurrence of this resistance: (1) disease resistant oysters are physiologically or genetically different from non-resistant ones, and (2) disease-resistant oysters acquired immunity through early exposure to the pathogens. These two hypotheses are probably mutually inclusive.

Although evidence for the development of acquired immunity in molluscs is far from satisfactory, there are several interesting findings. In 1964, Michaelson (1964) reported the production of a microacidial immobilizing substance by snails infected with *Schistosoma mansoni*. Acton and Evans (1968) found that the bacterophage T2 was cleared more rapidly from oyster (*C. virginica*) hemolymph after secondary injection than after primary injection. Feng and Stauber (1968) suggested that the precipitous reduction in the number of *Hexamita* sp. in resistant oysters 8 days post-injection might be attributed to the presence of acquired immunity. Furthermore, Hardy et al. (1977) demonstrated that exposure of oysters (*C. gigas*) to bacteria stimulated an increase substantially in the titre of bacterial agglutinin.

Disease problems in oysters and other bivalve species have stimulated interest to determine the feasibility of inducing acquired immunity to the pathogen *P. marinus* in American oysters, *Crassostrea virginica*. Like other invertebrates, bivalve molluscs do not appear to possess immunoglobulins. Phagocytosis is the principle mechanism by which bivalve molluscs normally defend themselves against invading pathogens and foreign materials (Cheng and Rifkin 1970; Cheng 1981; Cheng 1983). The importance of phagocytosis in determining the outcome of a disease has been established (Metchnikoff 1893; Sindermann 1971). The phagocytic activity of the host to invading pathogen is correlated with the degree of resistance (McKay and Jenkin 1970). Resistance is decreased by a lowering of phagocytic activity (Aarum 1967). In order to test the efficacy of immunization with a possible *P. marinus* vaccine, a technique was developed to measure the phagocytosis of *P. marinus* zoospores by oyster hemocytes. This paper describes the radiometric technique developed for this purpose.

Osmotic infiltration is a practical mass-immunization method which was originally developed by Amend and Fender (1976) for immunizing fishes. This method is less stressful on the animal and less time consuming than individual inoculation. Antigens are infiltrated into fishes during immersion of the animal in a hyperosmotic solution containing the antigen (Antipa and Amend 1977; Croy and Amend 1977; Bowers and Alexander 1981). Lewis and his associates (The University of the Sea, Vol. 15, No. 1, 1982, Texas A&M University; The University of the Sea, Vol. 14, No. 3, 1981, Texas A&M University) also successfully immunized shrimp against bacterial diseases by placing shrimp in hyposmotic water containing antigen. Since the osmotic infiltration technique has proven to be very effective and successful for mass-vaccination of small fishes and shrimp, we wanted to evaluate the osmotic infiltration technique for immunization of oysters. To examine whether oysters can take up antigens by osmotic infiltra-

tion, experiments were performed to determine the uptake of radiolabeled bovine serum albumin (^{14}C-BSA, Molecular weight = 69,000 daltons) and radiolabeled zoospore homogenate. Preliminary results from these experiments are reported in this paper.

MEASUREMENT OF PHAGOCYTOSIS OF *P. MARINUS* ZOOSPORES BY OYSTER HEMOCYTES

A summary of the sequence and procedure developed to measure phagocytosis of *P. marinus* zoospores by oyster hemocytes is shown in Figure 1.

Immunization and Maintenance of Oysters

Oysters (*Crassostrea virginica* (Gmelin)) were collected from upstream bars of the James River in Virginia. In this area, oysters have been protected by Dermo and MSX diseases by low salinity (5–14‰) (Andrews and Hewatt 1957; Chu, unpublished data). MSX and Dermo are believed to be inactive in salinity below 15‰. There were 2 groups of oysters (15 oysters per group): immunized and sham control. Oysters of the immunized group were injected intramuscularly with formalin-killed *P. marinus* zoospores twice (2.0×10^8 zoospores/oyster in 0.1 ml estuarine water) at a one week interval. Each of the sham control oysters was injected with 0.1 ml estuarine water. Both immunized and sham control oysters were held in a trough (210 × 60 × 15 cm L × W × H) filled with filtered (10 μm, 1 μm Cuno cotton filters) pasteurized estuarine water. Water in the trough was changed every two or three days. An algal diet (*Tetraselmis suecica*) was added to the trough daily (500 ml of $1-2 \times 10^6$ cells/ml per day). Twenty-four and 48 hrs after the second immunization, blood samples were taken from oysters (7 oysters/group/time period) for phagocytic activity measurement.

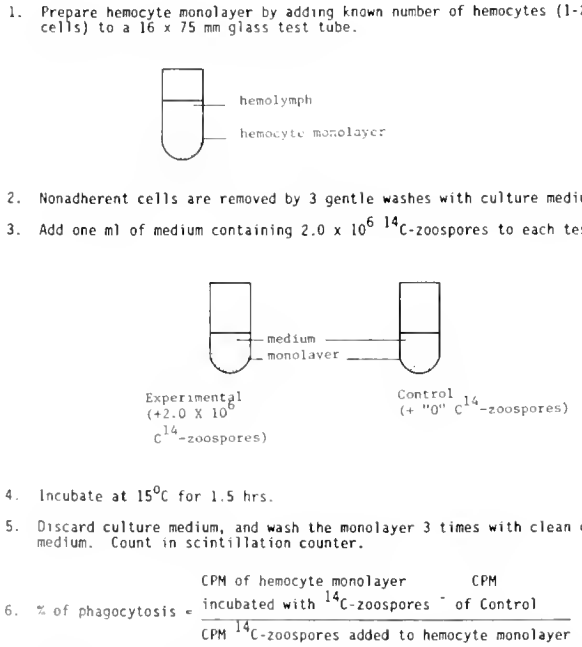

Figure 1. Procedure for quantifying phagocytosis of ^{14}C-zoospores of *Perkinsus marinus* by oyster hemocytes.

Collection of Oyster Hemocytes

Hemolymph was collected from oysters. A 27 gauge, 25 mm needle attached to a 1 ml sterile syringe was inserted in the adductor muscle of the oyster. Hemolymph was withdrawn and pooled at 4°C. The number of cells in the hemolymph was counted using a hemocytometer. About $1-2 \times 10^6$ cells in one ml of hemolymph were used for phagocytosis measurement.

Preparation of ^{14}C-labeled Zoospores

Presporangia and zoospores of *P. marinus* were cultured by methods described by Perkins and Menzel (1966). ^{14}C-labeled zoospores were obtained by culturing presporangia in 25 ml of 22‰ estuarine water containing 10 μCi ^{14}C-glycine (New England Nuclear, U.S.A.) at 27–28°C for 72–96 hrs. ^{14}C-labeled zoospores were harvested, treated with 0.3% formalin, and washed twice with sterile (0.22 μm filtered) estuarine water. ^{14}C-zoospores were then concentrated to a desired level for the phagocytosis study. The ^{14}C-zoospores obtained in this way contained $6.6-13.2 \times 10^{-2}$ dpm/spore. The percent of radioactivity leached from the zoospores after 24 hrs incubation in ^{14}C-glycine-free sea water was 0–25%.

Measurement of Phagocytosis

Known numbers of cells ($1-2 \times 10^6$ cells) in one ml of hemolymph were placed in 16 × 75 mm culture tubes and allowed to adhere at 15°C for 30 minutes. At the end of the time, nonadherent cells were removed by three gentle washes with minimal essential medium (MEM) and counted. About $1.5-2.0 \times 10^6$ ^{14}C-zoospores in 1 ml of MEM were added to the hemocytes and incubated at 15°C for 1.5 hours. Phagocytosis was stopped by discarding the supernatant and gently washing 3 times with MEM. Cell pellets were digested with 0.6 ml NCS (tissue solubilizer) at 50°C and the radioactivity in the aliquot was measured in 10 ml Aquasol with a scintillation counter. Percent of phagocytosis of ^{14}C-zoospores by oyster hemocytes was calculated using the following formula:

$$\%\ \text{of phagocytosis} = \frac{\text{CPM of hemocyte monolayer incubated with } ^{14}\text{C-zoospores} - \text{CPM of control hemocyte monolayer}}{\text{CPM } ^{14}\text{C-zoospores added to hemocyte monolayer.}}$$

Since the number of hemocytes placed in the glass tubes to prepare the hemocyte monolayer and the number of ^{14}C-zoospores added to the hemocyte monolayer are known, percent of phagocytosis can also be expressed in terms of number of ^{14}C-zoospores phagocytized by number of hemocytes. Counts of the number of nonadhering cells indi-

cated that about 95–97% of the hemocytes adhered. The phagocytic responses of hemocytes (2×10^6 cells) pooled from 7 immunized oysters and 7 sham control oysters employing this technique are shown in Figure 2. The results showed the uptake of ^{14}C-labeled zoospores by hemocytes sampled 24 and 48 hrs after the second immunization. The uptake of ^{14}C-labeled zoospores of *P. marinus* by hemocytes from immunized oysters was higher than hemocytes from control (non-immunized) oysters. It was speculated that a cellular response was elicited in oysters at 24 and 48 hrs after the second challenge with formalin-killed zoospores, but further study is needed to verify this speculation, and the specificity of the response has not been determined. The increased response of sham control at 48 hrs suggests a nonspecific reaction of oyster hemocytes.

Phagocytosis is usually measured by enumerating the number of hemocytes which have ingested bacteria (or the pathogen) or by measuring the optical density of abiotic particles (e.g. latex ring) ingested by oyster hemocytes (Anderson and Good 1976; Cheng and Sullivan 1984). The radiometric technique described in this paper is the first reported method to radiolabel an oyster pathogen and directly measure the phagocytosis of the radiolabeled pathogen by the oyster hemocytes. Phagocytosis includes processes of recognition, adherence, ingestion, destruction and disposal. Interaction of hemocytes and live or formalin-killed *P. marinus* zoospores has been examined with light phase contrast microscope, and both adhesion and ingestion were observed. It was assumed that the uptake of radioactivity by the oyster hemocytes was due to either adherence or ingestion. The application of this technique to measure phagocytosis of *P. marinus* spores by oyster hemocytes will be further evaluated.

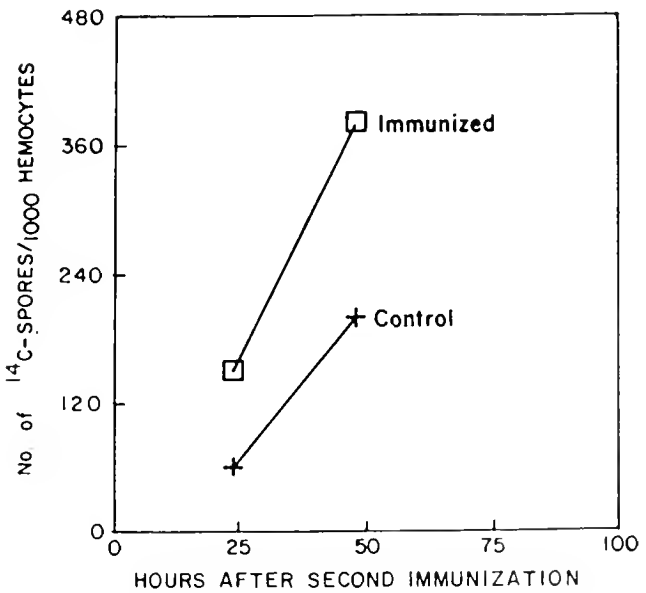

Figure 2. *In vitro* cellular phagocytic response of oyster hemocytes.

UPTAKE OF DISSOLVED AND PARTICULATE ANTIGENS THROUGH OSMOTIC INFILTRATION BY THE OYSTER, *C. VIRGINICA*

The size of oysters used for the osmotic infiltration experiments ranged from 2 to 3 cm shell height. Oysters were submerged individually for 1–3 hrs in hyposmotic water containing [^{14}C]-methylated bovine serum albumin (soluble antigen ^{14}C-BSA, molecular weight $\simeq$ 69,000 daltons, Amersham) or ^{14}C-labeled zoospore hemogenate (particulate antigen). The ^{14}C-labeled zoospore homogenate was prepared by disrupting the zoospores with sonifier cell disruptor (Model W185, Heat Systems—Ultrasonic Inc.). Hyposmotic water was prepared by lowering the salinity in which the oysters were held from 16‰ to 10‰ with chlorine free tap water. Uptake of ^{14}C-BSA by oysters submerged in water of the same salinity (16‰) was also determined. All the experiments were performed at room temperature ($\simeq$22°C), unless stated otherwise. To examine the effect of temperature on the uptake of antigens, the osmotic infiltration was performed at 18 and 30°C.

Results from the preliminary osmotic infiltration studies indicate that through osmotic infiltration the oyster can take up both ^{14}C-BSA and ^{14}C-labeled zoospore homogenate (Fig. 3 and Table 1). The uptake of antigen was correlated with the concentration of antigen added to the water (Figure 3). Elevated water temperature does not appear to increase but to decrease the antigen uptake; it was found that the uptake of C^{14}-BSA in oysters in water of 18°C was 2 times higher than in oysters in water of 30°C. A temperature of 30°C may stress the animals and retard the osmotic activity.

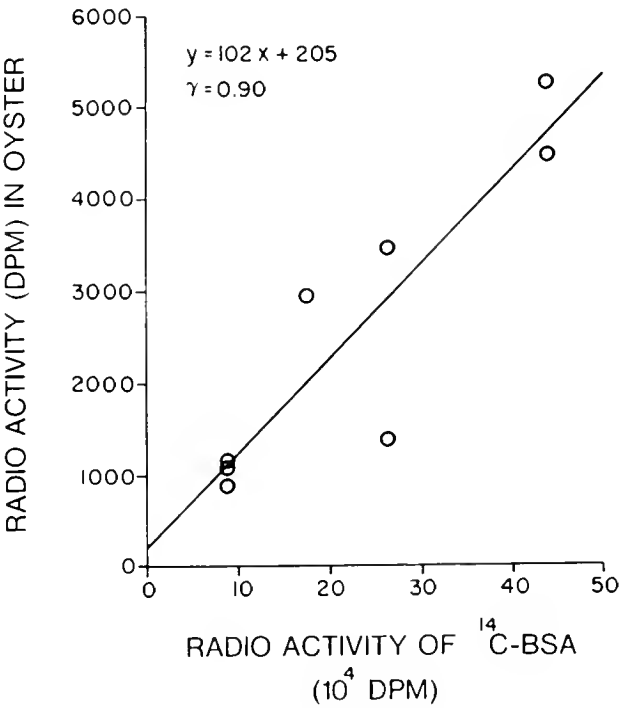

Figure 3. Uptake of ^{14}C-BSA by oysters through osmotic infiltration.

TABLE 1.

Uptake of radiolabeled zoospore homogenate by oysters*

Oyster	Radioactivity (DPM) of Zoospores Added to the Water	Radioactivity in Oysters (DPM)	% of Uptake
1	3896 (2.13×10^6 zoospores)	2022	51.9
2	3896 (2.13×10^6 zoospores)	1233	31.6
3	3896 (2.13×10^6 zoospores)	1875	48.3
$\bar{x} \pm SD$		1710.0 ± 419.5	43.9 ± 10.8
4	1047 (0.98×10^6 zoospores)	350	33.0
5	1047 (0.98×10^6 zoospores)	413	39.0
6	1047 (0.98×10^6 zoospores)	288	27.5
7	1047 (0.98×10^6 zoospores)	244	23.0
$\bar{x} \pm SD$		328.8 ± 73.7	30.6 ± 6.9

* Oysters were exposed to 2 different concentrations of ^{14}C-labeled zoospores from 2 different culture stocks at room temperature (22°C); exposure time was two hours.

TABLE 2.

Uptake of ^{14}C-BSA by oysters incubated in hyposmotic (10‰) and isosmotic (16‰) waters*

Oyster	Radioactivity (DPM) of ^{14}C-BSA	Radioactivity in Oysters	
		10‰	16‰
1	2.6×10^5	5738	
2	2.6×10^5	2830	
3	2.6×10^5	3922	
4	2.6×10^5		3297
5	2.6×10^5		4380
6	2.6×10^5		3373
7	2.6×10^5		1598
$\bar{x} \pm SD$		4163 ± 1469	3162 ± 1154

* Oysters were incubated at room temperature (22°C) for 3 hrs.

since the oysters were held in ambient water of 18–20°C prior to the experiment. Results also demonstrated that ^{14}C-BSA infiltrated into oysters held in water of the same osmotic concentration (Table 2). The uptake of C^{14}-BSA was similar to those immersed in hyposmotic water. The efficiency and reliability of the osmotic infiltration technique for immunization of oysters will need further investigation. The uptake of antigen in oysters could be the results of the synergy of osmotic infiltration, active transport (pinocytosis) and phagocytosis processes.

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RAPID DECLINE IN OYSTER CONDITION IN THE PATUXENT RIVER, MARYLAND

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ABSTRACT The meat condition index of a population of oysters in the Patuxent River, Maryland was determined monthly from February 1986 to February 1988. This period was characterized by dry weather and above average salinity which led to the spread of *Haplosporidium nelsoni* (MSX) into much of Maryland from Virginia, resulting in widespread high mortalities. The population sampled in this study showed no unusual mortality, but oyster condition declined significantly. It is unknown if this decline is related to sublethal infections of MSX, pollutants, or other factors, but the decline indicates a stress on the system. Routine monitoring of oyster condition could serve as a useful early warning mechanism for threatened populations.

KEY WORDS: Condition index, oyster, *Crassostrea virginica*

INTRODUCTION

After several good years of larval recruitment during the early and mid 1980s (Davis et al. 1981; Krantz and Davis 1983; Abbe 1988), the fishery for the oyster *Crassostrea virginica* (Gmelin) has reached the lowest level in Maryland in a century. In 1885 the Maryland harvest was 15×10^6 bu (Kennedy and Breisch 1981). By the early 1900s, production had declined to 4×10^6 bu, and from 1934 to 1984 the annual harvest averaged only 2.5×10^6 bu. In 1984 and 1985, landings were barely 1×10^6 bu. The 1986–87 oyster season produced about 9.8×10^5 bu, and the 1987–88 season may yield only half of that (C. Bonzek, Maryland Department of Natural Resources, pers. comm.).

In recent years, low harvests have followed periods of unusually high spat setting which was improved by above average salinity during several dry years. Unfortunately, the high salinity also allowed the invasion of the pathogenic protozoan *Haplosporidium nelsoni* (Haskin, Stauber, and Mackin) (MSX) from Virginia into Maryland where it generally does not occur (Rosenfield and Sindermann 1966; Andrews and Wood 1967). MSX is most prevalent where salinity is 20–25‰, but it is infectious at 15‰ (Andrews 1964; Ford 1985). It becomes less pathogenic as salinity decreases from 15 to 10‰ and apparently cannot tolerate salinities below 10‰ (Haskin and Ford 1982; Andrews 1983). MSX mortalities were quite high in the middle Chesapeake Bay during 1986 and 1987 as salinity remained above 15‰ most of this time. Therefore, although recruitment to the population remained high, the high rate of disease-related mortality has kept population densities and fishery yields low.

During this period of heavy disease mortality, we were able to observe, as part of an unrelated study, a major decrease in meat condition of oysters in the upper Patuxent River. Salinity in this area is often 6–8‰, but was 12–15‰ during 1986 and 1987. The oysters, however, have shown no unusual mortality.

METHODS AND MATERIALS

Ten oysters of similar size (means ranged from 79 to 97 mm; overall mean was 87.8 ± 4.8 mm) were collected monthly from February 1986 to February 1988 from the Holland Point oyster bar near Benedict, Maryland (Fig. 1). As part of a study of trace element concentrations in oysters, meat conditions were also determined. Oysters were cleaned of fouling organisms, scrubbed, rinsed in deionized water, and blotted dry. They were then measured for shell length, weighed whole, and shucked. Dry meat weights were determined and the empty valves weighed after 24 hr. Meat condition indices were determined using the methods of Lawrence and Scott (1982) according to the formula:

$$\frac{\text{dry tissue weight (g)}}{\text{shell cavity volume (ml)}} \times 100$$

where shell cavity volume (ml) is equal to the difference between the weight of the whole oyster (g) and the weight of the empty valves (g).

RESULTS AND DISCUSSION

The condition index is a unit-free number relating an individual oyster's soft tissue to its shell cavity volume. Although high values (above 10) generally indicate that oysters are in good physiological condition, low values do not necessarily indicate oysters in poor health because condition decreases whenever tissue is lost; spawning therefore results in a short term loss in condition. Long-term loss, however, may indicate stress from other sources such as pollutants, hypoxia, or disease.

Mean condition indices decreased from 10.8 in February 1986 to 5.7 in February 1988. The high and low during this time were 12.4 in April 1986 and 4.6 in October 1987, respectively (Fig. 2). Linear regression yielded a significant decline in condition ($p < 0.01$; $r^2 = 0.659$; $df = 24$). Oyster size (as shell length) was not related to the decline because size showed no change with time ($p > 0.20$; $r^2 =$

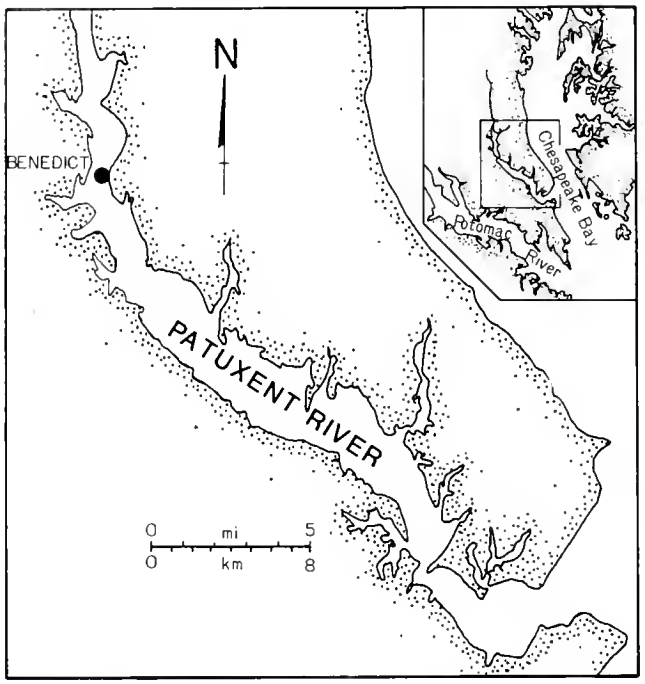

Figure 1. Location of Holland Point oyster bar (black dot) near Benedict from which oysters were sampled during 1986–88.

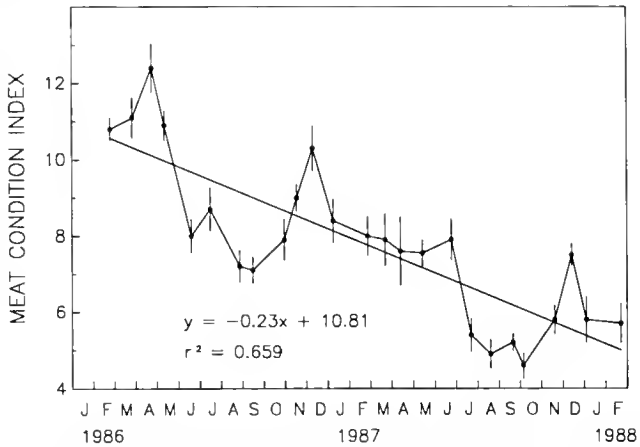

Figure 2. Mean meat condition indices of oysters sampled monthly from February 1986 to February 1988 from Holland Point bar. The regression line and its equation are also shown. (Vertical bars are standard errors of the mean.)

0.007; df = 24). The general patterns of 1986 and 1987 were similar and typical for this area of the Patuxent River (Abbe and Sanders 1986); we expect that these patterns were typical for oysters in much of Chesapeake Bay as well. On a seasonal basis, high values occurred early each year, followed by decreases in late spring or early summer, lows during late summer or early fall, and increases during fall (Fig. 2). These seasonal fluctuations are related to reproductive activity in spring and summer and glycogen storage in fall (Galtsoff 1964).

What is unusual about these 2 years is the overall decline in condition index, with a mean of 9.4 in 1986 and 6.7 in 1987. This decline occurred during a time of widespread disease mortality in Chesapeake Bay. It is unclear, however, whether any relationship exists between mortality and condition, and any attempt to relate them here would be speculative. No unusual mortality was apparent among the oysters on Holland Point bar; it has traditionally been too far upriver to be affected by MSX. Yet something has happened to cause this loss in condition.

We know that MSX has a deleterious effect on the feeding rate of oysters and can result in reduced condition index (Newell 1985), but we also know that contaminants in estuarine water can produce measurable differences in condition (Scott and Lawrence 1982). Were lowered conditions of Holland Point oysters typical of other populations in the Chesapeake? If so, reduced condition, possibly indicating a poorer physiological state, might help explain the high mortalities observed during 1987, because oysters under stress from any cause would probably be more susceptible to disease.

No attempt is made at this time to determine the cause of this declining condition, but the use of a simple index, as discussed by Lawrence and Scott (1982), has alerted us to a potentially serious situation. Scott and Lawrence (1982) suggested increased emphasis on the use of condition index over a wider geographical range and for longer periods of time to monitor the wellbeing of oyster populations. We intend to continue to monitor this population in the Patuxent River and urge others to consider the technique for other areas.

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ESTIMATING MORTALITY RATES IN THE ICELAND SCALLOP, *CHLAMYS ISLANDICA* (O. F. MÜLLER)

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ABSTRACT Annual natural mortality in the Iceland scallop, *Chlamys islandica* computed from percent occurrence of cluckers was found to be significantly higher ($P < 0.001$) on exploited beds (0.140 to 0.204) than on unfished grounds (0.024 to 0.084). In a heavily fished population the difference in rates for fully recruited ages (≥9 yrs) between two consecutive years is ascribed to localized fleet movements and provides a first estimate of indirect (incipient) fishing mortality (0.07) for the population. The difference between natural mortality rates for a population heavily fished and one in the virgin state, here estimated to be 0.047 provides a better estimate of gear-induced mortality. Depending on the type of gear used and the intensity of fishing effort, indirect fishing mortality was determined to vary from about 17% in the inshore Digby dredge to about 31% in the heavy, offshore New Bedford dredge, i.e. approximately four (3.9) and eight (7.7) times as many scallops perish as a result of encounters with fishing gear than through natural causes.

KEY WORDS: Scallop, mortality, *Chlamys islandica*

INTRODUCTION

The Iceland scallop, *Chlamys islandica*, has its main distribution within the subarctic zone (Ekman 1953) but fishable aggregations are found as far south as Nantucket off the coast of Massachusetts (Serchuk and Wigley 1984). This species, being a filter feeder, is most commonly found in areas characterized by strong currents. Fisheries for the species occur principally in Canada, Iceland, Norway, and to a lesser extent in the United States. More recently, a fishery has developed in western Greenland (S. A. Pedersen, Greenland Fisheries Research Institute, Tagensvej 135, 1, DK-2200 Copenhagen N. Denmark, pers. comm.). The mollusc is relatively small, seldom exceeding 110 mm in shell height (tangential dorso-ventral axis).

In Newfoundland (Canada), populations of the Iceland scallop are normally found in waters deeper than 55 m, usually on hard bottom with variable substrate composition largely consisting of sand, gravel, shell fragments, rocks, and boulders. A pulse fishery for the species occurs in the northeastern Gulf of St. Lawrence, where annual landings have been as high as 239 t meats (Naidu et al. 1982). Recently, a directed fishery for scallops developed offshore on St. Pierre Bank (Fig. 1). This area is unique in that two scallop species (Iceland and sea scallops (*Placopecten magellanicus*)) are found, frequently intermixed. Gear typically used in the Canadian inshore and nearshore fishery consist of Digby buckets (Fig. 2) fished either singly or in a "gang" of up to eight buckets spaced along a tow bar. In the offshore fishery large New Bedford type dredges (Fig. 2), frequently up to 4.8 m (16 ft) wide are employed. An empty 3.7 m (12 ft) dredge weighs about 0.7 t and upwards of 4 t when full of rocks (Royce 1946; Bourne 1964). Frequently, two such dredges are employed simultaneously, one on each the port and starboard. Fishing vessels, particularly those employing the heavier gear, are necessarily quite powerful. Tow duration is usually to gear saturation, time varying with scallop density. While the heavy, steel dredges customarily employed in harvesting scallops have long been suspected of causing damage to the benthos including targeted species, comparatively few studies have been conducted to assess their impact (Medcof and Bourne 1964; Caddy 1968, 1973; Gruffydd 1972). Caddy (1973), for example, estimated incidental mortalities to sea scallops *P. magellanicus* with an offshore dredge to be at least 13–17% per tow. This investigation provides estimates of non-yield fishing mortality in Iceland scallops.

MATERIALS AND METHODS

Systematic surveys for the Iceland scallop were conducted during 1980 and 1981 in the northeastern Gulf of St. Lawrence where an active commercial fishery had been underway (Naidu and Smith 1982). The surveys based on a systematic lattice design (Smith and Naidu 1981), were conducted to determine the distribution of scallops and to assess the suitability of the survey design for biomass estimation. Eleven latitudinal transects, each one nautical mile apart, were run in the target area. Stations were assigned at ½ mi. intervals along these lines. One hundred and three stations were occupied in 1980 but operational constraints reduced coverage to 59 in 1981. All tows were made with a gang of four toothless Digby buckets mounted on a single tow bar. Dredges were equipped with 64 mm (2.5 in.) rings and carried a 38 mm (1.5 in.) polypropylene mesh liner to increase retention of smaller scallops. The liner was frequently inspected and repaired or replaced as necessary. Each tow covered ¼ nautical mile with a 3:1 warp to depth ratio. Tow speed varied from 2.5 to 3.0 knots.

Dredges were hauled up at the end of each tow and the catch "bushelled" into baskets and weighed to the nearest

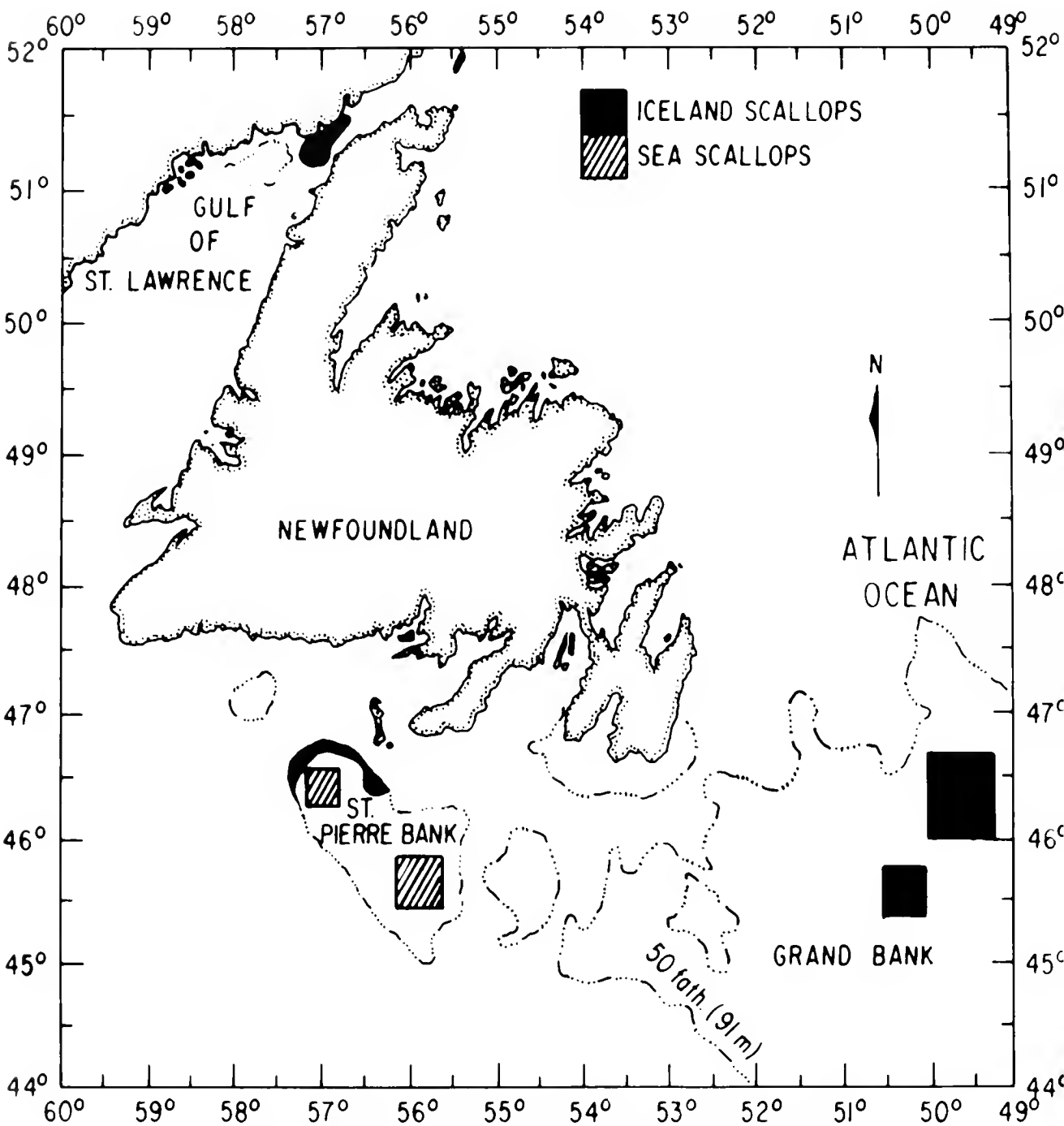

Figure 1. Map of Newfoundland (Canada) showing principal sampling areas.

kg. Individual shell heights were recorded (to the nearest mm) on either the whole catch, or a weighed random subsample, depending on the amount caught. All cluckers (persistent paired valves still attached at the hinge line) were counted and measured, again to the nearest mm. A tally was kept of animals so badly damaged that measurements were impossible (Fig. 3).

Marked cluckers were used to determine the rate of tow-induced disarticulation during typical ¼ mi. tows. These were completed in the same survey area in the northeastern Gulf of St. Lawrence. Experimental cluckers were measured and individually tagged (Naidu and Cahill 1985) to distinguish them from those that would be caught during these tows. To better simulate typical dredge tows experimental cluckers were interspersed or "seeded" into each bucket among 4–10 kg of live scallops before each tow. There were five experimental tows, each with 10 tagged cluckers in each of the four buckets. Seventy-five of the

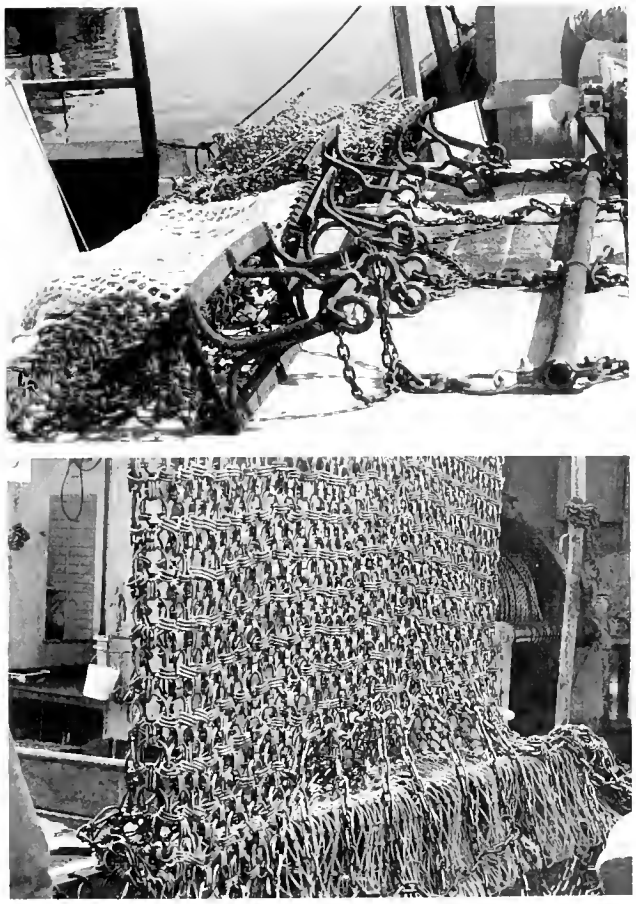

Figure 2. Digby scallop buckets (top) and a New Bedford offshore scallop dredge.

Figure 3. Typical damage to dredge-caught Iceland scallops.

tagged cluckers were of the gaping variety and the remaining 125 were collapsed but still intact at the hingeline (Fig. 4).

Detailed data were assembled on various fishery characteristics in the Gulf during 1980 and 1981. These included fishing positions, shell height composition of landings, and catch per unit of effort. Additional baseline data were gathered during independent research vessel surveys to determine areal distribution and abundance of the mollusc and from selectivity experiments. Data on the percent occurrence of Iceland scallop cluckers on unexploited beds on the Grand Banks of Newfoundland were available for one year only, but were derived from two separate cruises covering wide areas. Elsewhere, on St. Pierre Bank, frequency of cluckers relative to live captures was available for both the pre- and post-exploited phases.

Random samples of shells from the systematic line surveys in the northeastern Gulf of St. Lawrence were retained for age determinations. Rings on the left (upper) valve were employed in assigning ages and in back calculations to derive shell heights at age. An age-shell height key was constructed using the complete shell height-at-ring formation data (N = 2658; Table 1) and used to generate scallop ages at given shell heights. The 50% retention shell height for the 64 mm ring used in the Gulf *Chlamys* fishery is 70 mm, corresponding to a mean retention age of 8 yrs (Naidu et al. 1982). Nine-year-old scallops were considered fully retained by commercial gear.

Natural mortality

Natural mortality was computed directly from percent occurrence of cluckers (Dickie 1955) according to the equation:

$$M = 1 - e^{-(\frac{c}{t})(\frac{1}{L})365}$$

where M = annual natural mortality rate, c is the number of cluckers in a sample (adjusted to account for tow-induced disarticulation), L is the number of live scallops in the same sample, and t is the average time in days required for the valves of cluckers to separate naturally. Time required for natural clucker disarticulation (210.8 days) was experimentally determined by Mercer (1974). The age-height key was used to determine ages at given shell heights for both live and dead scallops and age-specific natural mortality rates calculated. These were separately computed for northeastern Gulf scallops for 1980 and 1981. For

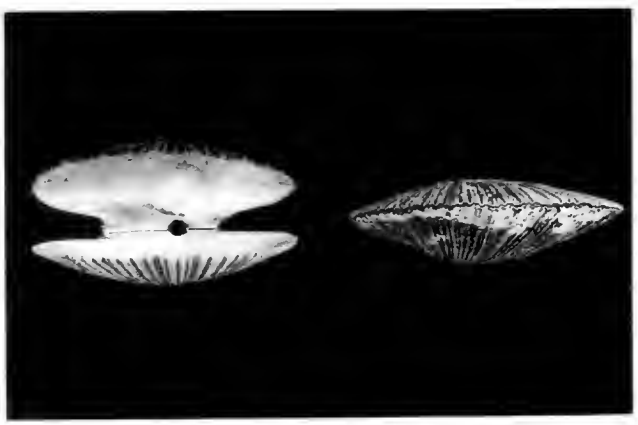

Figure 4. Gaping (left) and collapsed cluckers of the Iceland scallop.

TABLE 1.

Summary of back measurements of size-at-ring formation for 284 Iceland scallops taken in 1980 (tangential dorso-ventral distances) from the northeastern Gulf of St. Lawrence.

Ring no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Mean size (mm)	6.8	14.5	24.4	36.1	47.8	58.1	66.5	72.7	77.5	81.8	85.0	87.0	89.3	90.8
No. measurements	256	284	284	284	284	276	266	250	205	125	76	43	18	7
S.D. mean	1.6	2.9	4.3	5.3	5.7	5.6	5.6	5.4	5.5	5.7	5.2	5.2	5.3	5.1

Grand Banks and St. Pierre Bank only overall natural mortalities were computed.

Total mortality rate (Z) for Gulf scallops was calculated from commercial catch and effort data (Naidu et al. 1982).

RESULTS

Of the 200 tagged cluckers used to determine tow-induced disarticulation (75 gaping and 125 collapsed), 171 were retained (64 out of 75 gaping and 107 out of 125 collapsed, Tables 2 and 3). There was no difference ($P > 0.05$) in the mean size of the two categories: 80.8 ± 6.6 mm (SD), and 80.4 ± 7.2 mm for gaping and collapsed respectively. Neither was there a difference ($P > 0.05$) in the mean size of the two types of cluckers retrieved: 81.4 ± 6.6 mm versus 80.5 ± 7.2 mm. Loss of experimental cluckers during the tows was 15% for both categories. Frequency of tow-induced disarticulation was, as expected, higher in gaping than in collapsed cluckers in which hinge resilience had disappeared (29.7 vs 11.2%; Table 3), i.e. 89% of collapsed compared to 70% of gaping cluckers remained attached at the hingeline during tows with an overall mean of 82%. Unfortunately, data on the frequency occurrence of each clucker type on scallop grounds are not available. A predictive model was therefore constructed to evaluate the sensitivity of the mortality estimate (M) to varying representations of the two categories of cluckers and to adjustment factors computed therefrom. Disarticulation time (t) was allowed to vary from 50 to 300 days. The simulation showed M to decrease exponentially with t (Fig. 5). M values showed progressive convergence with increasing t and approached an asymtote towards high values of t. For t values greater than 200 days, varying the proportions of gaping to collapsed cluckers from one extreme (100% gaping) to another (100% collapsed) resulted in only small differences in M. As expected, M was relatively more sensitive to the adjustment factor used in correcting for tow-induced disarticulation than to various representations of the two types of cluckers (Fig. 5). Within the range of adjustment factors obtained empirically, a wide variation in M is predicted, particularly for small values of t. For the t value used in this study (210.8) a difference of up to 47% in the estimate is possible. Although records were not kept on the frequency of the two types of cluckers it was obvious that there were many more collapsed cluckers on the scallop grounds than of the gaping variety. Also, cluckers appear to persist much longer in the collapsed state than in the gaping condition. This results in fewer gaping cluckers in the population. While the higher disarticulation rate among gaping cluckers would lead to a high-biased estimate of M, their relative numbers would tend to underestimate it. Given the reduced sensitivity of M to t and to various representations of the two categories of cluckers in the context of their persistence over time, it seemed reasonable on empirical grounds to use the weighted average of 1.221 in this first attempt to adjust clucker numbers to account for tow-induced disarticulation (Table 3).

Comparisons of the rates of disarticulation within individual buckets for each tow and between separate tows (Table 2) show greater variability in disarticulation in the latter. Whereas overall rates for individual buckets varied narrowly between 16.7 and 20%, those for the five separate tows ranged from 5 to 39%. These observations suggest that type of bottom and composition of substrates may have an effect on the fate of cluckers entering the dredge. There

TABLE 2.

Number of cluckers retained per tow in simultaneous 4-bucket tows and numbers (in parentheses) forcibly disarticulated.

Tow No.	Bucket A	Bucket B	Bucket C	Bucket D	Totals	% disarticulating by tow
1	10 (1)	8 (1)	9 (2)	10 (0)	37 (4)	10.8
2	10 (1)	9 (0)	10 (0)	10 (1)	39 (2)	5.1
3	9 (1)	10 (1)	10 (4)	6 (2)	35 (8)	22.9
4	4 (2)	8 (3)	8 (3)	9 (3)	28 (11)	39.3
5	8 (2)	9 (3)	8 (0)	7 (1)	32 (6)	18.8
Totals	41 (7)	44 (8)	45 (9)	42 (7)	171 (31)	
% disarticulating	17.1	18.2	20.0	16.7		18.1

TABLE 3.

Disarticulation based on original condition. Total numbers of each type used, recoveries and numbers forcibly disarticulated (parenthesized).

Tow No.	Clocker numbers						Adjustment factor
	Initial			Recaptured			
	Gaping	Collapsed	Totals	Gaping	Collapsed	Totals	
1	21	19	40	19 (3)	18 (1)	37	1.121
2	9	31	40	9 (1)	30 (1)	39	1.054
3	12	28	40	11 (5)	24 (3)	35	1.297
4	18	22	40	13 (7)	15 (4)	28	1.647
5	15	25	40	12 (3)	20 (3)	32	1.232
Totals	75	125	200	64 (19)	107 (12)	171 (31)	
% disarticulating				29.7	11.2	18.1	1.221
Adjustment factor				1.422	1.126		

is a slight but insignificant positive correlation ($r^2 = 0.15$, $P > 0.05$) between numbers disarticulating and catch weight (Tables 2 and 4). No correlation between disarticulation rate and depth ($r^2 = 0.01$, $P > 0.05$) was discernable within the narrow depth range examined (Table 4); indeed none was expected.

Overall, ratios of cluckers to live scallops in each of the three geographically discrete populations varied from less than two percent on St. Pierre Bank to 13.2% for the Gulf of St. Lawrence (Table 5). Annual natural mortalities for unexploited stocks of Iceland scallops in the Newfoundland area varied from 0.025 to 0.084. Computed values were consistently lower than those for exploited populations. The overall mean by averaging values from Grand Banks (1982) and St. Pierre Bank (1976, 1978) was 0.047 (or 5%). Frequency of cluckers in the Gulf population decreased significantly ($P < 0.001$) to 8.7% in 1981 from 12.2% the previous year. Although clucker numbers remained relatively low on St. Pierre Bank, an increase was evident in 1983 soon after an active commercial fishery had commenced in 1982, albeit for the sea scallop, *P. magellanicus*. Although mortalities in exploited contagions for both scallop species remained somewhat high through 1985, beds unfished on the Bank continued to register low natural mortalities (Table 5). As expected, the distribution of cluckers showed wide spatial variation, with inordinately large numbers being evident in some areas (Fig. 6). That there is a correspondence between sea scallop clucker numbers and fishing activity is further confirmed by their abundance in relation to total removals by year (Table 6). Mean numbers of sea scallop cluckers per tow from areas for which both research and commercial catch data are available in any year were significantly correlated to the catch in that year ($r^2 = 0.85$, $P < 0.05$). Although a decrease in the mean numbers per tow of cluckers of the Iceland scallop was clearly evident during the same period, the

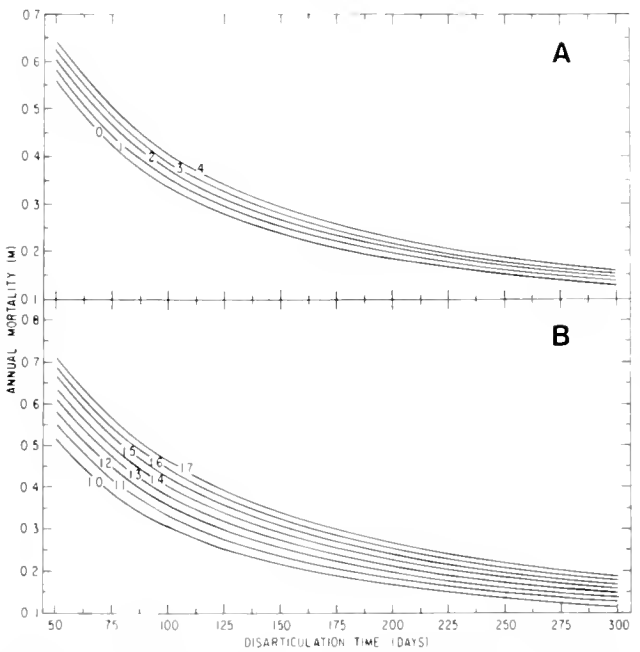

Figure 5. (A) Simulated trend with disarticulating time of natural mortality using varying representations of gaping and collapsed cluckers (0 = 100% gaping, 0% collapsed; 1 = 75% gaping, 25% collapsed; 2 = 50% gaping, 50% collapsed; 3 = 25% gaping, 75% collapsed and 4 = 0% gaping, 100% collapsed). (B) Simulated trend with disarticulating time of natural mortality using the range of adjustment factors obtained experimentally.

TABLE 4.

Scallop catch (whole weight, kg) by individual bucket and mean catch per tow.

Tow No.	Depth Range (m)	Catch weight by bucket				Mean catch/tow
		A	B	C	D	
1	75	9.0	8.5	9.0	8.5	8.8
2	77–80	7.0	10.0	8.5	7.0	8.1
3	69–73	12.5	12.5	12.5	9.5	11.8
4	68–73	8.3	12.5	9.5	12.5	10.7
5	69–77	15.5	14.0	16.0	14.0	14.9
Mean/bucket		10.5	11.5	11.1	10.3	

TABLE 5.

Estimates of annual natural mortality for three populations of *Chlamys islandica* from Newfoundland (M_1, based on cluckers only; M_2, based on cluckers and crushed scallops).

Year	Location	Gear	Tow distance (nautical mi.)	Live scallop nos.			Clucker nos.		M_1	M_2
				Measured	Crushed (%)	Total	Observed	Adjusted (%)		
1980	NE Gulf of St. Lawrence[2]	Digby × 4 (lined)	0.25	9,950	175 (1.7)	10,125	1,095	1,336 (13.2)	0.204	0.231
1981	NE Gulf of St. Lawrence[2]	Digby × 4 (lined)	0.25	16,947	396 (2.3)	17,343	1,235	1,507 (8.7)	0.140	0.177
1982	Grand Banks[3]	New Bedford (unlined)	1.0–1.5	17,297	3,158 (15.4)	20,455	434	529 (2.6)	0.044	0.309
1982	Grand Banks[3]	New Bedford (unlined)	1.0	11,138	1,279 (10.3)	12,417	340	415 (3.3)	0.056	0.232
1976	St. Pierre Bank[1]	Digby × 4 (lined)	0.25	1,235	55 (4.3)	1,290	53	65 (5.0)	0.084	0.155
1976	St. Pierre Bank[1]	Digby × 4 (unlined)	0.25	1,442	60 (4.0)	1,502	43	52 (3.5)	0.058	0.126
1983	St. Pierre Bank[2]	New Bedford (lined)	0.5	4,583	114 (2.4)	4,697	448	547 (11.6)	0.183	0.221
1983	St. Pierre Bank[2]	New Bedford (unlined)	1.0	6,069	1,143 (15.8)	7,212	585	714 (9.9)	0.158	0.411
1985	St. Pierre Bank[2]	New Bedford (unlined)	0.5	42,261	6,906 (14.0)	49,167	2,494	3,043 (6.2)	0.102	0.335
1985	St. Pierre Bank[1]	New Bedford (lined)	0.5	3,597	377 (9.5)	3,974	62	76 (1.9)	0.033	0.196
1985	St. Pierre Bank[1]	New Bedford (unlined)	0.5	2,410	324 (11.9)	2,734	45	55 (2.0)	0.034	0.238
1985	St. Pierre Bank[1]	New Bedford (lined)	0.5	2,570	255 (9.0)	2,825	54	66 (2.3)	0.040	0.194
1985	St. Pierre Bank[1]	New Bedford (unlined)	0.5	1,894	236 (11.1)	2,130	25	31 (1.5)	0.025	0.217

[1] Localized tows associated with selectivity studies (unexploited grounds).
[2] Tows restricted to commercially attractive contagions (exploited grounds).
[3] Exploratory or survey tows covering large areas (unexploited grounds).

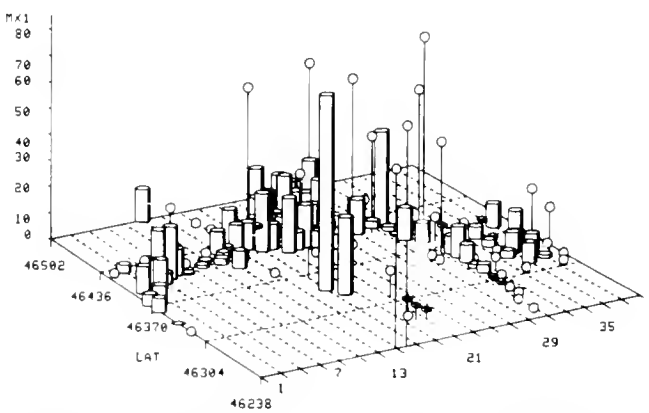

Figure 6. Spatial distribution of annual natural mortality, M (×100) in the Iceland scallop computed from ratio of cluckers to live scallops over a portion of St. Pierre Bank in 1985. Balloons, boxes and columns correspond to areas with catches of 0–49, 50–99, and over 100 live scallops/tow respectively.

correlation between their numbers and landings was not statistically significant ($r^2 = 0.68$, $P > 0.05$).

The frequency with which animals were crushed during capture shows a correspondence with the type of gear em-

TABLE 6.

Relationship between mean clucker numbers/tow and removals from St. Pierre Bank. Number of research vessel tows for which data on clucker incidence are available from exploited areas is parentbesized.

Year	Landings (MT)	Mean clucker no./tow	
		Iceland	Sea
1982	717	6.271 (59)	1.538 (78)
1983	594	5.500 (86)	1.341 (88)
1984	413	5.556 (99)	0.856 (118)
1985	53	4.543 (79)	0.834 (169)
1986	19	1.682 (44)	0.480 (74)

ployed (Table 5). The heavier offshore dredges crushed greater numbers of scallops. The frequency and severity of damage inflicted was greatest with the offshore unlined commercial gear. In independent studies, it has been shown that overall damage to scallops increases with distance towed and that for a given tow distance, frequency of damage is greater in tows completed over rough bottom than those over smooth grounds (Naidu, unpublished).

Age determinations using annual rings on the shell were reliable only to about 13 yrs. Beyond that there were problems with interpretation. Recaptures of live tagged scallops after nearly a decade (9 yrs.) in the wild showed no shell growth (Naidu, unpublished). Growth rings may merge with one another or become laminated to conceal size increments related to age (Naidu et al. 1982).

Age-specific natural mortality in the Gulf during two consecutive years (1980 and 1981) increased with age (Tables 7 and 8). Annual mortality rate computed from the ratio of cluckers to live scallops was substantially lower during the second year of the survey. An analysis of the covariance of the logarithmic transformations of M on age for 1980 and 1981 pointed to no significant differences in slopes ($P > 0.05$) but elevations were different ($P < 0.01$). Total mortality (Z) for the 1980–81 period increases with age (Table 9) as a result of increasing natural and fishing mortalities (weighted mean of 0.742 corresponding to an F of 0.533).

DISCUSSION

In most fisheries literature, particularly stock assessments, the rate of natural mortality for a given population is assumed to remain constant throughout the adult history of the animal. This rate is factored into various yield computations either for simplicity in modelling, or more frequently, simply because data on age-specific mortality are simply lacking. In scallops, we are fortunate in not only being able to age them readily but in distinguishing those that die naturally from those removed by the fishery where the valves are deliberately and forcibly separated at the hinge-line during shucking to remove the adductor muscle or "meat."

Senescence alone cannot account for all natural deaths, particularly in an area where an active capture fishery is underway as was the case in the Gulf of St. Lawrence where significant removals had occurred in both 1980 and 1981. This study attempts to address the non-yield mortality resulting from fishing. Indirect mortality occurs at various stages during the process of fishing. Not every animal in the gear path is caught or retained. Some scallops elude capture gear and recover completely from the "blitz." Others may be crushed *in situ* as the heavy dredge moves along the sea bottom or may be inadvertently forced into the substrate and become debilitated to face certain death. Shell damage to uncaptured sea scallops (*P. magellanicus*) has been directly observed through diving (Caddy 1968). In addition to physical damage to scallops within the dredge, active muscle adductions associated with escape responses, particularly during saturation tows, lodge grit and shell fragments into the scallop. These contaminants cause various degrees of mantle retraction and prolonged moribundity, sometimes no doubt resulting in death. Damaged or weakened scallops are more likely engaged by predators. Caddy (1968) reported numerous scavenging benthic predators to be attracted by the passage of the scallop drag. Further damage is inflicted when scallops are dumped on deck. This involves inverting the scallop rake

TABLE 7.

Age-specific natural mortalities computed from ratio of cluckers to live scallops in the Gulf of St. Lawrence, 1980. Observed clucker numbers are adjusted upwards by a factor in the range of 1.054 to 1.647 ($\bar{x}$ = 1.221) to allow fur tow-induced disarticulation (C_a = adjusted clucker numbers; M_o and M_a = observed and adjusted mortalities).

				Adjustment factor											
				1.054		1.121		1.232		1.297		1.647		$\bar{x}$ = 1.221	
Age	No. cluckers observed	No. live	M_0	C_a	M_a	C_a	M_a	C_a	M_a	C_a	M_a	C_a	M_a	C_a	M_a
5	6	127	.079	6	.083	7	.088	7	.096	8	.101	10	.126	7	.095
6	26	288	.145	27	.152	29	.161	32	.175	34	.184	43	.227	32	.174
7	68	952	.116	72	.122	76	.129	84	.141	88	.148	112	.184	83	.140
8	152	1911	.129	160	.135	170	.143	187	.156	197	164	250	.203	186	.155
9	220	2387	.148	232	.155	247	.164	271	.178	285	.187	362	.231	269	.177
10	219	1808	.189	231	.198	245	.210	270	.228	284	.238	361	.292	267	.226
11	167	1187	.216	176	.226	187	.239	206	.259	217	.271	275	.330	204	.257
12	129	691	.276	136	.289	145	.304	159	.328	167	.342	212	.413	158	.326
13	54	300	.268	57	.280	61	.295	67	.319	70	.333	89	.401	66	.317
14	39	129	.408	41	.424	44	.444	48	.475	51	.493	64	.578	48	.472
Σ5–14	1080	9780	.174	1138	.182	1211	193	1331	.210	1401	.220	1778	.270	1320	.208
Σ9–13	789	6373	.193	832	.202	885	.214	973	.232	1023	.243	1299	.297	964	.230

TABLE 8.

Age-specific natural mortalities computed from ratio of cluckers to live scallops in the Gulf of St. Lawrence, 1981. Observed clucker numbers are adjusted upwards by a factor in the range of 1.054 to 1.647 ($\bar{x}$ = 1.221) to allow for tow-induced disarticulation (C_a = adjusted clucker numbers; M_o and M_a = observed and adjusted mortalities).

Age	No. cluckers observed	No. live	M_o	Adjustment factor 1.054 C_a	1.054 M_a	1.121 C_a	1.121 M_a	1.232 C_a	1.232 M_a	1.297 C_a	1.297 M_a	1.647 C_a	1.647 M_a	$\bar{x}$ = 1.221 C_a	$\bar{x}$ = 1.221 M_a
5	9	199	.075	9	.079	10	.084	11	.092	12	.097	15	.121	11	.091
6	29	512	.093	31	.098	33	.104	36	.114	38	.119	48	.149	35	.113
7	94	1836	.085	99	.089	105	.095	116	.103	122	.109	155	.136	115	.103
8	197	3700	.088	208	.093	221	.098	243	107	256	.113	324	.141	241	.106
9	267	4302	.102	281	.107	299	.113	329	.124	346	.130	440	.162	326	.123
10	239	2999	.129	252	.135	268	.143	294	.156	310	.164	394	.203	292	.155
11	174	1768	.157	183	.164	195	.174	214	.189	226	.198	287	.245	212	.188
12	117	948	.192	123	.202	131	.213	144	.231	152	.242	193	.297	143	.230
13	58	368	.239	61	.250	65	.264	71	.286	75	.298	96	.362	71	.283
14	30	134	.321	32	.335	34	.352	37	.380	39	.395	49	.472	37	.377
Σ5–14	1214	16766	.118	1279	.124	1361	.131	1495	.143	1576	.150	2001	.187	1483	.142
Σ9–13	855	10385	.133	900	.139	958	.148	1052	.161	1109	.169	1410	.209	1044	.160

allowing the catch, including rocks, to free fall from heights frequently exceeding 3 m (10 ft.). Dredge-caught scallops nearly always contain a few animals so severely damaged as to provide no yield (Fig. 3). In fact, these may be considered to be 'instant' cluckers.

It is apparent, however, that the frequency of damage is greater in the unlined offshore dredge than in lined gear normally employed in research vessel tows. Lined gear cushions the severity of impact between scallops and steel, thus minimizing damage. Sometimes, scallops are voluntarily or inadvertently returned to the sea bed after varying periods of deck exposure. Culling of scallops becomes necessary to ensure meat counts are nonviolative (regulated number of scallop meats per unit weight, e.g. 40 meats/500 g). Depending on the severity of damage, these may suffer subsequent mortality. Sorting scallops from trash seldom exceeds ½ hr. Mortality among scallops returned to the sea bed within a reasonable time is low, at least in minimally damaged sea scallops, *P. magellanicus* (Naidu, unpublished). Medcof and Bourne (1962) estimated mortality in sea scallops resulting from prolonged air exposure to range from 2 to 20%. Iceland scallops maintain tighter shell closure than do sea scallops, perhaps enabling them to tolerate longer periods of air exposure. Scallops that survive turbulent encounters with fishing gear register the accompanying stress through the deposition of a shock ring usually resulting from mantle damage or temporary mantle retraction. Depending on the severity of impact, this may be a mild shock ring, as is commonly observed in several exploited scallop species or it may be sufficiently violent to require replacement of portions of the shell margin. This results in various changes in the anatomical configuration of the shell and leads to some deformity (Fig. 7). It is evident, however, that types of damage commonly seen may only result from extrinsic man-made causes.

TABLE 9.

Estimates of Z and F for Iceland scallops for 1980/81 in the Gulf of St. Lawrence. (Total mortality coefficient, Z is from Naidu et al. 1982.)

Age	Z	$\bar{M}$	F
9–10	0.463	0.150	0.313
10–11	0.731	0.190	0.541
11–12	0.964	0.222	0.742
12–13	1.290	0.278	1.012
13–14	1.684	0.300	1.384

$Z_{(9-13)}$ = 0.7417 $\bar{M}$(1980–81) = 0.195 $\bar{F}$(1980–81) = 0.533

The difference between an average weighted M from a population heavily fished and one in the virgin state was used to estimate indirect fishing mortality. While the absolute values reported in this paper may be subject to change by a number of factors, the overall difference should remain unchanged so long as disarticulation time and the factor used to adjust for tow-induced disarticulation remain unchanged. Simply, it is the "added" non-yield component that is being estimated. The mean adjustment factor used in this study to compensate for tow-induced disarticulation (1.221) must be considered tentative. It recognizes the unequal representation of the two types of cluckers. To have assumed an equinumerical representation would have required adjusting observed numbers by a factor of 1.274 which would result in high-biased mortality estimates. *In situ* sampling by means more sophisticated than dragging would be required to estimate actual numbers of the two types of cluckers. Also, as already noted, it is likely that

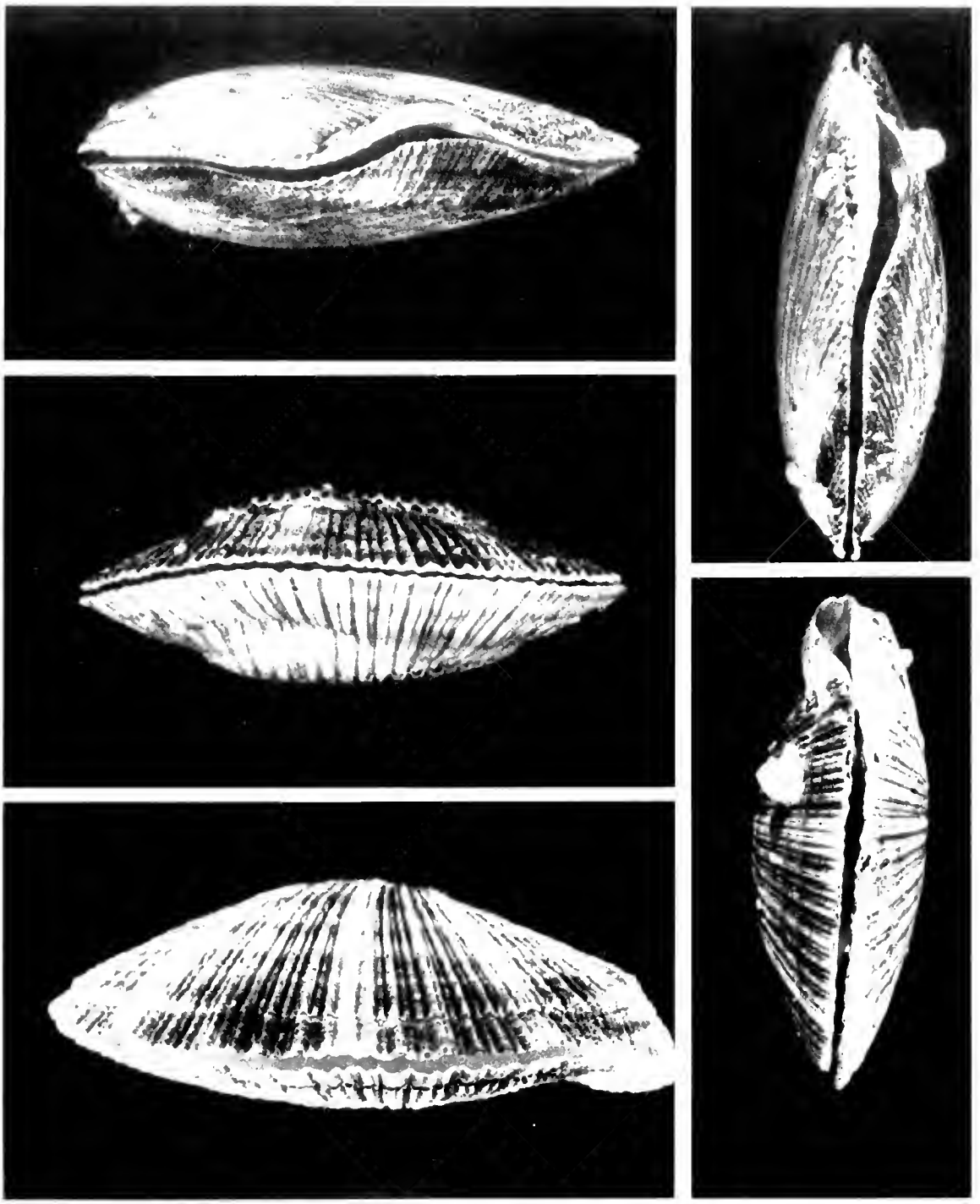

Figure 7. Common shell deformities in Iceland scallops captured from a heavily exploited bed in the northeastern Gulf of St. Lawrence.

disarticulation rates will vary with type of bottom and with capture gear. The simple adjustment for clucker numbers by a factor of 1.221 is based on ¼ mi. tows in the Gulf of St. Lawrence. We may expect greater numbers to disarticulate during longer tows. Baseline estimates of M for the Grand Banks and St. Pierre Bank must therefore be considered underestimates. Some of the constraints implicit in the calculation of natural mortality rates from clucker to live scallop ratios have been discussed by previous authors (Dickie 1955; Merrill and Posgay 1964; Mercer 1974). Most of them tend to overestimate M. Among these is the assumption that both cluckers and live scallops are equally vulnerable to capture. While precise figures on the efficiency of Digby dredges for capturing *Chlamys* are not available, it is known to vary, depending upon bottom type, between 5 to 15% for the sea scallop, *P. magel-*

lanicus (Dickie 1955). Iceland scallops are probably more prone to being captured as they are unrecessed and byssally attached to bottom substrates (Gruffydd 1976, 1978). Examining a population of Iceland scallops in Balsfjord in northern Norway, Vahl and Clausen (1980) concluded that nearly all scallops were attached by the byssus and that swimming is a relatively rare occurrence. In the laboratory, 76% (155 of 205) of Iceland scallops (43–93 mm, shell height) were found to be byssally attached, whereas only 9% (8 of 88) of sea scallops (59–70 mm) were similarly attached (Naidu and Meron 1986). As active escapement would be minimized, it is probable that the assumption of equal catchability is reasonable. It is likely, however, that long-dead cluckers are more likely to disarticulate than recently-collapsed cluckers. This would cause an underestimation of their numbers in the catch thereby introducing a low bias in the mortality estimate. On the other hand, the entire population is not equally vulnerable to fishing effort at any time (Caddy 1975). This unequal distribution of fishing effort will inflict a mosaic of M, depending on the duration and intensity of that effort. This, too, will underestimate M, particularly when it is computed from clucker to live numbers pooled from a large area. Detailed examination of the spatial distribution of M on St. Pierre Bank over three years supports this assumption. Commercially attractive contagions subjected to the most effort produced highest ratios of cluckers to live scallops providing direct confirmation of fishery-induced mortality. This may explain the "graveyards" containing very high proportions of cluckers observed here and reported elsewhere such as those on Georges Bank (Posgay 1962). He suggested that in a heavily fished area, live sea scallop numbers will be reduced faster than cluckers, thereby creating an artificially high clucker to live scallop ratio. It is difficult to reconcile this with his earlier observation that cluckers may be more catchable than live scallops. The disproportionate numbers of cluckers reported from exploited populations more likely result from mortality inflicted from repeated tows.

At the time observations were made, the northeastern Gulf fishery had been expanding and moving away from grounds heavily exploited to virgin beds, but within the same general area (Naidu et al. 1982). Careful monitoring of the fishery in both 1980 and 1981 pointed to fleet movements based on localized depletion and declining catch per unit of effort. Nevertheless, the fishery was confined to within a 100 nautical mi^2. Mortality computed from a clucker to live scallop ratio in the second year would include a measure of incipient, fishery-induced mortality in the population. The overall difference in weighted means between the two years of fully-recruited ages (>9+ yr) provides a minimum estimate of indirect fishing or non-yield mortality in this fishery. For purposes of assessment, particularly for yield-per-recruit considerations, due cognizance should be taken of this non-yield mortality, here estimated to be at least 0.07. F, then approximates to 0.463 from 0.533 (i.e. 0.533–0.07).

Until very recently there was no commercial fishery for scallops on either St. Pierre Bank or the Grand Banks of Newfoundland. Rates of natural mortality computed for unexploited stocks were considerably lower than those in the Gulf of St. Lawrence with an overall mean of 0.047. If we assume that the ratio of cluckers to live scallops in unfished populations provides a better estimate of intrinsic natural mortality for the species, then indirect fishing mortality computed for the exploited Gulf population would be 0.157 (0.204–0.047) and 0.093 (0.140–0.047) in each of 1980 and 1981 respectively (Table 5). Corresponding non-yield mortality (gear-induced) would be 0.184 (0.231–0.047) and 0.130 (0.177–0.047). The absence of a marked increase in the instantaneous mortality coefficient on unfished beds over a nine-year period on St. Pierre Bank to the order of magnitude observed on exploited beds provides corroborative evidence supporting the hypothesis that fishing itself initiates an additional mortality in the population. A fishery for sea scallops commenced on St. Pierre Bank in 1982. Concomitantly, but not surprisingly, natural mortality of Iceland scallops computed from clucker to live scallop ratios, particularly in heavily fished contagions became elevated and has been reported as high as 0.206 (Naidu and Cahill 1984). Meanwhile, the Iceland scallop fishery in the northeastern Gulf of St. Lawrence has expanded into hitherto unexploited grounds off Labrador. As expected, pre-exploitation natural mortality computed from the ratio of dead to live scallops was considerably lower than those separately determined by Mercer (1974) and Naidu et al. (1982) and has been reported to be as low as 0.066 (Lanteigne et al. 1986). Previous estimates no doubt included the mortality component ascribable to fishing. More recently, Lanteigne and Davidson (1987) noted a 74% difference in the frequency of cluckers in this fishery over a two-year period during which significant removals had occurred. Repetitive tows over productive grounds may explain the observed disparity between the two years. There was probably considerable overlap between the areas surveyed in the second year and where an intense fishery had occurred one year previously.

The absence of statistical correlation between frequency of cluckers and spatial removals of Iceland scallops from St. Pierre Bank (Table 6) is not surprising. The directed fishery on St. Pierre Bank was aimed at sea scallops only. Iceland scallops are frequently intermixed with sea scallops and when caught in large numbers were considered to be a nuisance bycatch and discarded. There was a directed fishery for Iceland scallops in 1984 (Naidu and Cahill 1985), but this was spatially well removed from the areas of sea scallop exploitation.

The majority of crushed scallops are discarded and provide little yield to the fishery. The ones categorized in this study as being damaged most certainly perish when returned to the sea bed. These may be considered as contributing to the net clucker population. When these are added to the mortality computations, it becomes apparent that

total non-yield mortality (natural and indirect fishing mortality) could be as high as 20% in lined Digby dredges and possibly as high as 34% in the unlined New Bedford dredge. Clearly, the ratio of dead to live scallops in unfished populations provides a more realistic measure of intrinsic natural mortality for the species. This being so, annual indirect fishing mortality must be estimated to be at least as high as 0.184 (0.231–0.047) or 17% and possibly as high as 0.364 (0.411–0.047) or 31% for the Digby and New Bedford dredges respectively, i.e. approximately four (3.9) and eight (7.7) times as many scallops die from encounters with fishing gear than through natural causes. Incidental mortality to Iceland scallops with the offshore dredge is approximately twice the value (13–17%) reported for sea scallops, *P. magellanicus* (Caddy 1973). The higher rate may be due to the more sedentary nature of the species as well as the greater propensity to being byssally attached, sometimes at exceedingly high densities.

Annual natural mortality reported here for unexploited stocks of Iceland scallops (5%) is approximately one-half the previous estimate of 11% (Mercer 1974). His estimate for the exploited Gulf of St. Lawrence population probably includes the moiety of non-yield mortality inflicted by fishing. The lower rate reported in this paper appears to be compatible with the expected longevity of this arctic-boreal species.

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DAILY GROWTH RINGS IN JUVENILE SAUCER SCALLOPS, *AMUSIUM BALLOTI* (BERNARDI)

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ABSTRACT The number of pigmented rings occurring in the growth increment of tagged juvenile saucer scallops *Amusium balloti* (Bernardi) in Shark Bay, Western Australia was closely related (r = 0.996) to the number of days at liberty. The number of rings was always slightly less than the number of days, because of the loss of small amounts of shell from around the lip during the recapture process. The nature of the pigment forming the rings, which are laid down in the outer, calcitic layer of the shell, is unknown. The rings become very closely packed when animals mature and enter their first spawning season, which provides a means of distinguishing recruits from older year classes. Total ring counts may provide a means of direct ageing of recruits while growth per ring gives a permanent record of the daily rate of growth.

KEY WORDS: Scallop, Pectinidae, *Amusium*, daily growth, growth rings

INTRODUCTION

The shells of a variety of recent and fossil bivalves have been shown to have marks which delineate increments of growth claimed to relate to various time periods. The most widely recognized is the annual growth ring, but daily and sub-daily marks have also been reported (Barker 1964, Broom and Mason 1978, Deith 1985, Lutz and Rhoads 1980 (review)). These marks may be structural changes on the surface of the shell (e.g. as in *Argopecten irradians*, (Lam.) (Wheeler, *et al*, 1975), *Pecten diegensis* (Dall) (Clark, 1968)) or internal marks which are only visible in thin sections or acetate peels (e.g. as in *Mercenaria mercenaria* (Linn.) (Panella and McClintock, 1968), *Cerastoderma edule* (Linn.) (Richardson *et al*, 1981)).

Supporting evidence for the validity of some of the claims for the time periods represented by the increment between the marks has, however, not always been produced. Gruffydd (1981) examined the production of supposed daily ridges by *Pecten maximus* (Linn.) under experimental conditions and found that the rate of production of ridges was not always daily and that it was particularly affected by temperature and shell size.

The outer surface of scallops of the genus *Amusium* are smooth and polished, with the left valve being brown to deep red and the right valve white (Habe 1964). The colour of the left valve of *A. balloti* (Bernardi) from Western Australia comes from concentrically arranged, fine, pigmented lines on a pale background. In the juvenile zone of shell growth the rings are readily resolved under a dissecting microscope, but in the more distal parts of the shells of mature animals the pigmented rings blend together. Specimens from the east coast of Australia also show fine, pigmented rings in the juvenile areas of the left valve, although the overall effect is of a darker shell as the rings are darker and there is some pigmentation between the rings. This paper reports the observation that the number of these pigmented rings in the growth increment of tagged juvenile *A. balloti* from Shark Bay is very closely related to the number of days at liberty and provides evidence that they are laid down daily.

METHODS

(i) *Tag-recapture*

Three groups of individually tagged scallops were released on the commercial scallop trawling grounds in Shark Bay, Western Australia (Lat. 25°00'S; Long 113°30'E) in the course of studies on growth and mortality. Orange PVC tags (''Dymo'' tape, Esselte Dymo) were applied to the shell using a cyano-acrylate glue (''Supa-Glue'', Selleys). Scallops were captured by trawling using the research vessel ''Flinders'', measured, tagged and returned to the sea within 1–4 hours. Except for brief periods during the sorting of the trawl and the measuring and tagging, scallops were stored in running sea water in a deck tank.

The three groups of animals were at liberty for differing amounts of time (Table 1). Recaptures of Group 1 animals were made by commerical vessels, while recaptures of the other two groups were made by R. V. ''Flinders''. Exact dates were available for all recaptures by ''Flinders'', but only 67 of the 140 commercial vessel recaptures had known recapture dates.

(ii) *Ring Counting*

As a result of the loss of a small amount of the shell around the lip at the time of capture, most recaptured scallops show a small step in the otherwise smooth surface of the shell, corresponding to the size at which they were tagged. Many also show a reddish flaring of pigment for 1 to 2 mm over the surface of the shell, but the more darkly pigmented rings are still visible through this flaring. The number of rings on the left valve of recaptured juveniles was counted under a dissecting microscope from the tagging ''step'' to the ventral edge of the shell along a line drawn from the umbo to the most distant part of the lip (shell height axis) (Figure 1). All counts were done by the

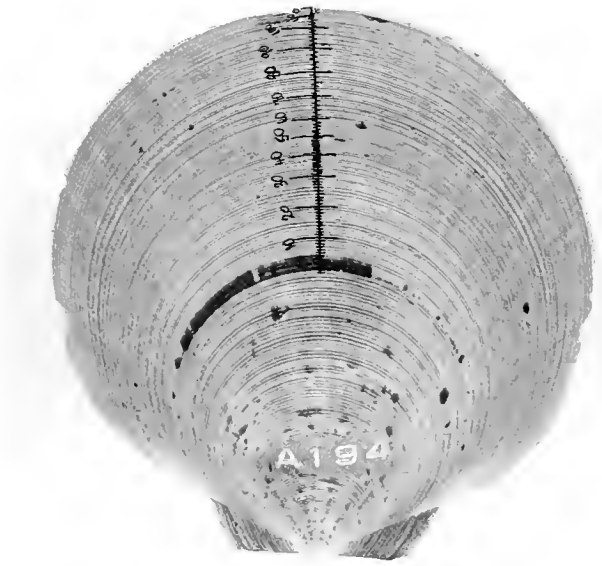

Figure 1. Recaptured *A. balloti* with ink marks highlighting rings along shell height axis. Note flaring of pigment at the tagging "step". Tagged: 7 November, 1984—Size: 50 mm; Recaptured March, 1985 —Size 94 mm. (Mag ×0.76)

author. The rings, which are present as a reddish-brown pigmented line approximately 0.15 to 0.25 mm wide on a pale background, were marked with a fine ink line to prevent mis-counting.

RESULTS

The pigmented rings of juvenile scallops are separated by up to 0.4 mm of unpigmented or weakly pigmented shell and are readily separated at low power under a dissecting microscope. However the outer band of rings of sexually mature scallops (i.e. scallops greater than about 90 to 95 mm shell height) are usually too closely packed to separate reliably. Also, animals tagged as immature scallops may reach maturity and have an outer band of rings which are too compacted to count if they are recaptured after long periods.

Of the 67 recaptures of Group 1 animals with known numbers of days liberty (Table 1), only 36 had rings which were sufficiently separated to permit counting over the whole growth increment. Of these 36 animals, 35 were juveniles at the time of tagging, with initial sizes of 36–78 mm. One animal (initial size 93 mm) was mature at the time of tagging, but the rings in the growth increment of 8 mm could just be resolved.

Most of the animals in which ring counts could not be done were mature animals, in which all rings in the growth increment were compacted. However, a few were juveniles which had matured during the time at liberty and had rings near the shell margin which were too compacted to resolve. With the 12 recaptures of group 2 animals, four scallops (initial sizes 88–96 mm) were mature animals and had

TABLE 1.

Release and recapture data for tagged *Amusium balloti*.

	GROUP		
	1	2	3
Date released	November 1984	September 1985	November 1985
Date recaptured	March 1985	November 1985	November 1985
Days at liberty	107–140	49–65	4–12
Number released	1000	157	500
Size range of releases (mm)	32–114	33–104	60–115
Number recaptured	67[1]	12	451
Size range of recaptures (mm)	83–108	58–100	60–115
Number suitable for ring analysis	36	8	6

[1] Number for which exact recapture date known.

rings which were too tightly packed to resolve and data were available only from eight juveniles (initial sizes 37–51 mm).

Although there were 451 recaptures of group 3 animals (Table 1), all the larger animals (>85 mm initial size) showed no recognisable growth increment for the brief period (4 to 12 days) for which this group was at liberty. Most scallops of smaller initial size showed the fragmentary remnants of newly-formed shell around the shell margin, but only six individuals (initial sizes 60–73 mm) retained a sufficiently undamaged rim of this delicate new shell for analysis.

The relationship between the number of pigmented rings from the tagging "step" to the ventral margin of the shell and the number of days at liberty was very close to 1:1 (Figure 2). The correlation coefficient between the number

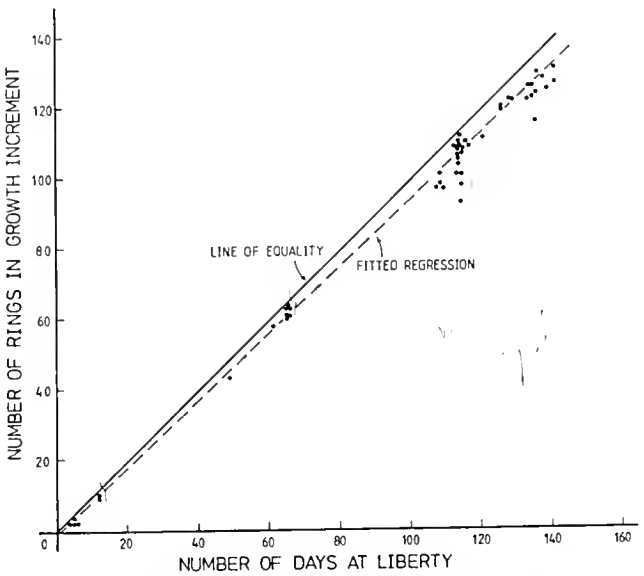

Figure 2. Number of rings in the growth increment of tagged *A. balloti*. Regression line is: Number of Rings = −1.0 + 0.939 (Number of Days).

of pigmented rings and the number of days at liberty (0.996) was significant at the 0.1% level. However, in all cases there were marginally fewer rings than days and the discrepancy was greater and more variable for the Group 1 animals, which had long periods at liberty.

This shortfall in the number of rings is considered to occur primarily as a result of the loss of shell from around the lip during the recapture of scallops by trawling. The thin shell of *A. balloti* is reinforced by internal radial ribs, but these do not reach right to the margins of the valves. As a consequence there is between 1 and 3 mm of un-reinforced lip, depending on the size of the shell, which is only approximately 0.15 mm thick (in scallops of 40–50 mm shell height) to approximately 0.35 mm thick (in scallops of 90–100 mm). The un-reinforced lip usually breaks off in a horseshoe shaped strip when scallops are spilled from the cod-end of the trawl. This was a particular problem with the recaptures of Group 1 animals from commercial vessels, where the cod-end contents can be very heavy.

The fitted regression line—

$$\text{No. of Rings} = -1.0 + 0.939\ (\text{No. of Days})$$

(Figure 2) explained 99.1% of the sum of squares. There was, however, a significant partial correlation between the size at tagging and the number of rings after the number of days had been taken into account, with animals of large initial size having a greater difference between the number of days at liberty and the number of rings. This source of bias may result from (i) a greater loss of rings by large scallops nearing maturity in which the loss of the same amount of shell causes a greater loss of rings than for immature scallops with less compacted rings, or (ii) blurred or mis-counted rings in large scallops entering maturity.

The rings visible on the left valve of *A. balloti* result from a band of pigmented laid down in the outermost shell layer. This layer (Figure 3) is composed of micro-crystalline calcite approximately 0.05 mm thick (at about 45 mm from the umbo) to approximately 0.13 mm thick (at about 90 mm from the umbo), overlaying a crossed-lamellar middle layer (terminology of Taylor *et al.* 1969) of calcite. Banding is visible in this middle layer and results from the differential reflection of incident light, presumably as a result of alternation in the direction of orientation of the crystal bundles. This banding is at a higher frequency than the pigmented rings and there was not any regular relationship between the banding in the middle layer and the pigmented rings in the outer layer. The nature of the pigment forming the rings in the outer layer is unknown, but is currently under investigation.

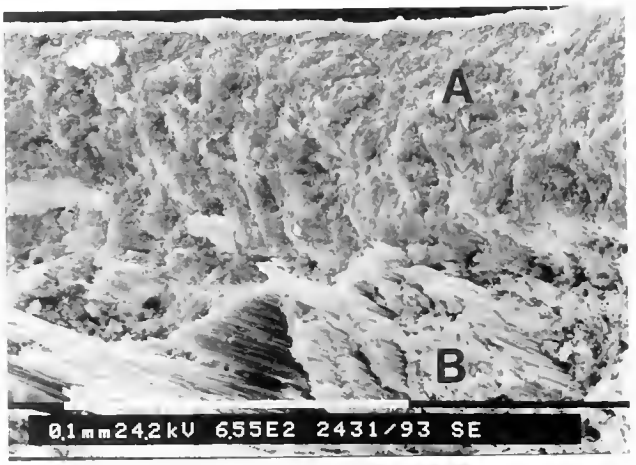

Figure 3. Electron micrograph of fracture along the shell height axis of *A. balloti* A = microcrystalline, calcitic outer layer; B = crossed-lamellar, calcitic middle layer.

DISCUSSION

Clark (1974) noted from experiments on a variety of pectinids that ridges were formed nearly, but not always, daily and that the daily periodicity of ridge formations was preserved only under the best conditions. Gruffydd (1981) examined the production of possible daily ridges by *Pecten maximus* under four light regimens and at two temperatures. He found that ridge production was not always daily and that it was particularly affected by temperature. There was, however, no consistent effect of the various photoperiods. He also found that the production of ridges around the margins of the shell varied with the size of the shell and that larger scallops produced more ridges over a given time period.

The observation on the relationship between the number of rings in the growth increment of tagged *A. balloti* and the number of days at liberty comes from animals of a limited initial size range growing under normal environmental conditions between September and March at one point in the species' range. These limitations are, however, dictated by the nature of the annual cycle of *A. balloti* in Shark Bay. New recruits (0+ age group, 30+ mm shell height), arising from a spawning season beginning in April, are first catchable in trawls around September of each year. Juveniles grow rapidly over the period September to March, by which time the bulk of the recruits reach a size of 90 to 95 mm and begin to enter sexual maturity (Joll, unpub. data). Consequently the time of year when juveniles are available is limited. Even late recruits, which only achieve a size of around 70–75 mm by March, begin maturing and show closely packed rings from March onwards. In only 1 mature animal was it possible to count the rings laid down in the growth increment. This animals was a late recruit and the rings, although distinguishable, were still very closely packed.

The distribution of *A. balloti* in Western Australia is from Shark Bay to Esperance (Lat. 34°'S Long. 122°'E) and specimens from throughout this range all show a similar pattern of markings of the left valve, although there are local variations in the intensity of colour. It is not known if

the rings observed in shells from these other locations also reflect daily growth or whether local environmental conditions cause a variation in their frequency of deposition. Specimens from Hervey Bay, Queensland (25°00'S; Long 152°30'E) of the species reported as *A. japonicum balloti* (Bernardi) by Dredge 1981 and as *A. japonicum balloti* Habe by Williams and Dredge 1981 also show distinct rings in the juvenile parts of the shell. However, the rings are much darker and, in addition, there is some pigmentation of the inter-ring spaces so that the overall effect is of a much more darkly coloured left valve.

The reason for there being fewer rings than days is considered to be most likely an artefact of post-capture handling, rather than a failure of the animals to lay down a ring on some days or a steady production of rings at a lower than daily frequency. The failure of the larger animals (>85 mm) from group 3 to grow any new shell over the short period that these animals were at liberty indicates that tagging may sometimes result in a brief cessation of growth in larger animals. However, nearly all the smaller animals showed the fragmentary remains of new shell deposition indicating that, for the size range of scallops considered, tagging shock was probably not a major factor reducing the number of rings produced.

The data indicate that the rings produced by juvenile *A. balloti* growing in the Shark Bay environment are of daily origin. Back- counting of rings from the outer margin of juveniles may, therefore, be used to determine the date of deposition of a ring. There will be some error in dating caused by the loss of shell from the lip if scallops are recaptured by trawling, but for rings within the range of the present data (i.e. within about 140 rings of the edge), a correction based on the regression could be applied. The distance between rings will give a record of the daily rate of growth on that date. Although there is some flaring and patchiness in the pigmentation in the first 5–10 mm of the shell, it is possible to count the number of rings on the left valve almost back to the umbo. On the assumption that the daily rhythm of ring formation is maintained in very small animals it would be possible to directly age juveniles by total ring counts. The close-packing of rings which occurs when animals mature and enter their reproductive season would prevent the direct ageing of older shells. However, the presence of this zone of closely-packed rings provides a means of distinguishing the immature recruits from the older year classes.

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The possibility that the rings represented daily growth was first suggested by S. Garcia. X-ray diffraction and thin sections to identify the composition of the various layers were done by B. Logan. J. Kuo assisted with the electron microscopy. Critical comment on the manuscript was given by J. Penn and N. Caputi.

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SEASONAL CHANGES IN OXYGEN CONSUMPTION OF THE GIANT SCALLOP, *PLACOPECTEN MAGELLANICUS* (GMELIN)

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ABSTRACT Rates of oxygen consumption ($\dot{V}O_2$) by the giant scallop, *Placopecten magellanicus* were measured monthly over a period of fifteen months. In addition, scallops were acclimated to a series of temperatures (T_a) in the laboratory and the rates of oxygen consumption monitored. In acclimated animals, $\dot{V}O_2$ increased with experimental temperatures with a concomitant decrease in Q_{10} value. Although the $\dot{V}O_2$ of scallops from the field was consistently higher than values obtained from acclimated scallops at similar temperatures, the general trend was in keeping with rates which varied with the environmental temperature. It was shown that the seasonal changes in respiration rate are intimately related to changes in the gametogenic cycle with the highest rates exhibited during the summer months (ripening of the gonads) and the lowest rates during the winter months. While the observed changes in metabolic rate generally follow the changes in environmental temperature, it is suggested that seasonal changes in food availability and reproductive stage have a greater affect on $\dot{V}O_2$ than temperature *per se*.

KEY WORDS: Scallop, *Placopecten magellanicus*, oxygen consumption

INTRODUCTION

The giant scallop, *Placopecten magellanicus*, represents one of the major fisheries in the Gulf of Maine. The species supports a large commercial fishery throughout its range and is currently considered as a prime species for aquaculture efforts. In spite of its economic importance, a recent review of the existing literature on this species (Shumway et al., in preparation) and the development of a preliminary model for the giant scallop ecosystem by Campbell (1985) revealed a number of aspects of the biology of this species that are still in need of investigation. These information gaps severely limited our ability to accurately model the system and included such basic data as seasonal changes in fecundity, growth rate, food availability, respiration rates and the effects of temperature on these parameters. A number of studies were undertaken to fill these gaps and the results have been reported elsewhere (Langton et al., 1987; Shumway et al., 1987; Schick et al., 1987; Barber et al., 1988; Schick et al., 1988a,b).

There are few data available on respiration rates of scallops in general, or *P. magellanicus* in particular. Vahl (1978), Shafee (1982), Shafee and Lucas (1982), Barber and Blake (1985), MacDonald and Thompson (1986a,b) and Bricelj et al. (1987) have all reported on seasonal changes in the metabolic rate in various scallop species and their results are summarized in the Discussion.

In a recent series of papers, MacDonald and his coworkers (1985a,b; 1986a,b; 1987) reported on the influences of temperature and food availability on the ecological energetics of *P. magellanicus* from Newfoundland. In his studies, water depth was used as a model for variable food supply and temperature. Water depth *per se* was not of particular interest, but rather the conditions at those depths. Although his station depths were only separated by approximately 20m, he was able to demonstrate marked differences in growth rates, gamete production, reproductive effort and other parameters as a result of differences in food and temperature. Our studies extend the depth factor (and associated environmental factors) considerably in that our stations range from approximately 20 to 180 m.

Since the peculiarities of any given environment affect the fishery locally, it is important to establish a comprehensive data base for individual areas if fishery management is to be efficient. Further, before any major aquaculture efforts can be undertaken, it is essential to have a firm understanding of the species' biology and the effects of variations in environmental factors on their performance. The majority of energy losses, or 'costs of living' (Sibley and Calow, 1986) can be measured as heat losses or respiration rates. In the present paper, we report on the seasonal changes in respiration rate for *P. magellanicus* in coastal Maine waters. The study is part of an ongoing research program designed to establish such a data base for *P. magellanicus* in Maine waters and the subsequent production of a model to describe growth and spawning in this species.

MATERIALS AND METHODS

Specimens of the sea scallop, *Placopecten magellanicus* Gmelin, were collected by divers at a depth of approximately 20m, from the lower Damariscotta River on a monthly basis between October 1984 and January 1986. Immediately after capture, the animals were transported to the laboratory, scrubbed free of epiphytes and maintained in running seawater from Boothbay Harbor prior to use in experiments. Vahl (1978) found that oxygen consumption in *Chlamys islandica* decreased during the first 20 days in the laboratory. Preliminary experiments indicated that no differences in rates of oxygen consumption ($\dot{V}O_2$) were apparent between the day of capture and up to 4 weeks after capture, as long as the temperature remained constant.

Since it was our intention to monitor, as closely as possible, the changes in $\dot{V}O_2$ under ambient conditions, measurements were made within 1–2 days of capture. Seawater temperatures at the collection site were within 2°C of the seawater in the laboratory and all experiments were run at ambient temperatures. Each month, $\dot{V}O_2$ was determined on scallops of a wide size range (0.01–18g dry tissue weight; approximately 10–130 mm shell height). The number of individuals measured varied (see Table 1). Dry tissue weights were obtained by oven drying to constant weight at 60°C for 24–48h.

Rates of oxygen consumption were determined for individual scallops using a Radiometer oxygen electrode in a closed system (Taylor and Brand, 1975; Shumway, 1983). Preliminary experiments indicated that $\dot{V}O_2$ was independent of oxygen tension (PO_2) only to approximately 70% saturation. Similar results have been shown for other species of scallops (van Dam, 1954; Vahl, 1978; MacKay and Shumway, 1980). Therefore, ambient PO_2 was not allowed to drop below approximately 80% saturation. Sexes were not separated. Since the animals were freshly collected and $\dot{V}O_2$ measurements taken immediately, the rates reported for the seasonal study are assumed to represent a 'routine' rate of oxygen consumption (see Bayne, 1976; Bayne and Newell, 1983).

Results are expressed as least squares regression according to the formula:

$$Y = aW^b$$

where Y is the predicted rate of oxygen consumption in ml oxygen hour^{-1}, W is the dry tissue weight in g, a is the intercept and b is a constant. All regression and statistical analyses were carried out on an IBM 370 computer using SAS programs (SAS, 1985).

For experiments to determine the effects of acclimation temperature on the scallops, animals were collected as above and maintained in ambient seawater and constant temperatures for 3 weeks prior to use in experiments. No food other than that which was available in the seawater supply was provided. For temperature acclimation which involved large changes in temperature, a step-wise series of acclimations was carried out whereby animals were maintained at an intermediate temperature for at least a week prior to being subjected to the final temperature of acclimation. This procedure eliminated mortalities due to temperature shock. Metabolic rates (routine) were measured as described above.

TABLE 1.

Parameters of the regression equations relating oxygen consumption ($\dot{V}O_2$; ml $O_2 \cdot h^{-1}$) to tissue dry weight (W; g) for *Placopecten magellanicus*. Data were fitted to the equation: $\dot{V}O_2 = aW^b$. Values preceded by an * are significantly different ($P < 0.05$) from the previous value. Values of b are given ± s.e.

DATE	b	a	r^2	n	T (°C)
20 Oct 1984	0.838 ± 0.029	0.363	0.992	19	10
27 Nov 1984	0.740 ± 0.039	*0.304	0.969	12	9
28 Dec 1984	0.714 ± 0.052	*0.220	0.949	12	6
29 Jan 1985	0.761 ± 0.049	*0.069	0.964	11	1
26 Feb 1985	0.755 ± 0.057	*0.196	0.951	11	4
29 Mar 1985	0.752 ± 0.037	*0.283	0.976	12	5
25 Apr 1985	0.848 ± 0.026	*0.259	0.990	13	8
25 May 1985	0.862 ± 0.062	*0.344	0.960	10	11
3 Jul 1985	0.837 ± 0.053	*0.386	0.968	10	17
31 Jul 1985	0.837 ± 0.037	0.399	0.985	10	19
5 Sep 1985	0.820 ± 0.030	0.428	0.984	14	16
1 Oct 1985	0.831 ± 0.104	*0.361	0.875	11	15
31 Oct 1985	0.814 ± 0.039	*0.382	0.973	14	11
15 Nov 1985	0.736 ± 0.039	*0.281	0.962	16	9
10 Jan 1986	0.740 ± 0.081	*0.162	0.903	9	3

RESULTS

Figure 1 shows the weight-specific rates of oxygen consumption for scallops acclimated to a series of experimental temperatures. There was a steady increase in the rate of oxygen consumption with increasing temperature coupled with a decrease in the calculated Q_{10} value. These data have been used to calculate the 'expected' $\dot{V}O_2$ at the various environmental temperatures (shown in Figure 2). With the exception of January, the observed rates of oxygen consumption were higher than the predicted values; however, the general trend was in keeping with rates that varied with the environmental temperature. Similar Q_{10} values for routine metabolic rate were reported for *C. varia* by Shafee (1982).

The monthly rates of oxygen consumption by *P. magellanicus* are summarized in Table 1. While the slopes of the lines are not significantly different as a group or individually, significant differences ($p < 0.01$) between levels of $\dot{V}O_2$ were found. The seasonal changes in $\dot{V}O_2$ are summarized in Figure 2 where it can be seen that the oxygen consumption rates generally followed the changes in environmental temperature. There were two major exceptions to this trend: 1) during the late winter and early spring where oxygen consumption rates increased at a much more rapid rate than would be predicted from the temperature changes alone and 2) during the late spring and early summer when rates of oxygen consumption remained fairly constant despite a fairly steep rise in environmental temperature. In addition, two significant decreases in $\dot{V}O_2$ occurred between March and April (when the temperature actually increased by 3°C) and between August and September (when the temperature only decreased by 1°C). Both of theses decreases are significant ($p < 0.05$) and are indicated in Figures 2 and 3 by arrows.

DISCUSSION

Metabolic rate in scallops has been studied by few workers. Vahl (1978) monitored the changes in metabolic rate of the Iceland scallop, *Chlamys islandica* (O. F.

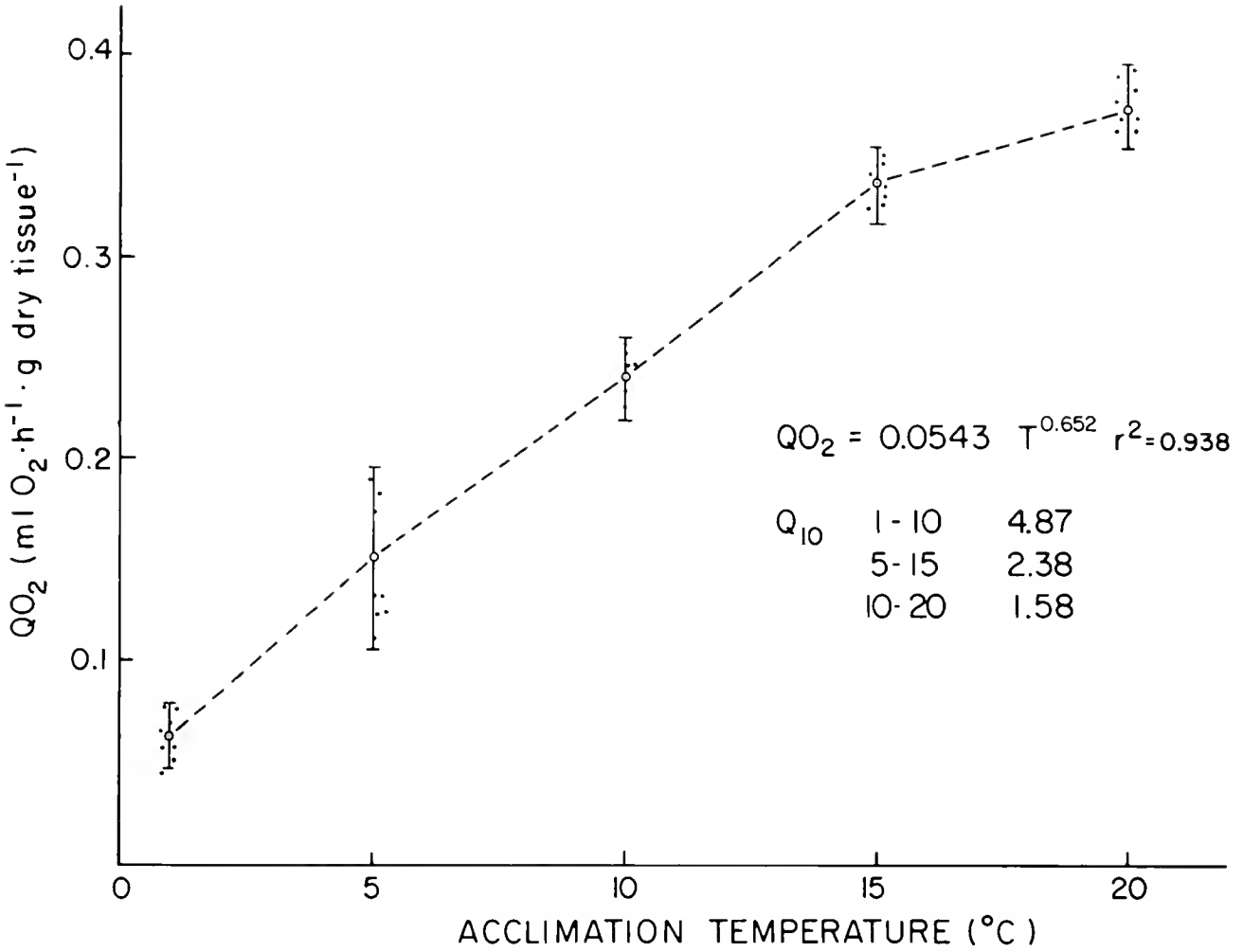

Figure 1. $\dot{V}O_2/T_a$ curve for *Placopecten magellanicus* over the range of normally experienced temperatures. Data are plotted for a standard scallop of 1 g dry tissue weight.

Muller) throughout the year. In addition, he determined seasonal changes in the relationship between body size and respiration rate. His results showed that the rate of oxygen uptake increased rapidly in the beginning of April, reached maximum levels in late April and May and thereafter decreased. This corresponds to the later part of the growth period of both shell and gonad in this species. He concluded that the seasonal variations in oxygen consumption exhibited by *C. islandica* were not explained by the seasonal variations in temperature but more likely were due to seasonal variability of the food supply. In addition, he showed significant seasonal variation in the dependence of oxygen consumption upon body weight. The exponent of the allometric equation relating $\dot{V}O_2$ to body weight for the period May-February was 0.78 while the exponent for the period March-April was approximately 0.90.

Shafee (1982) reported a common slope of 0.72 for all seasons in the Black scallop, *Chlamys varia*. He demonstrated a marked seasonal fluctuation in respiration rate with highest values in August/September and lowest values during February/March corresponding to periods of high temperature/peak gonad development and low temperature and little or no gonad activity respectively. Similarly, Bricelj *et al.* (1987) found that the oxygen consumption of the bay scallop, *Argopecten irradians irradians* (Lamarck) closely paralleled seasonal changes in water temperature. They showed that temperature explained 93% of the seasonal variation in metabolic rate with minimum values recorded in January/February and maximum values during June/July.

In the only published account on *P. magellanicus*, MacDonald and Thompson (1986) measured seasonal changes in metabolic rate and found no significant differences in weight exponents (common slope = 0.89), but significant differences in metabolic rates between seasons. Measured rates were lowest during January-May and much higher during summer, June-September. Further, they found differences with depth in that rates for scallops from shallow water were highly correlated with water temperature whereas those from deeper water (31 m) were not.

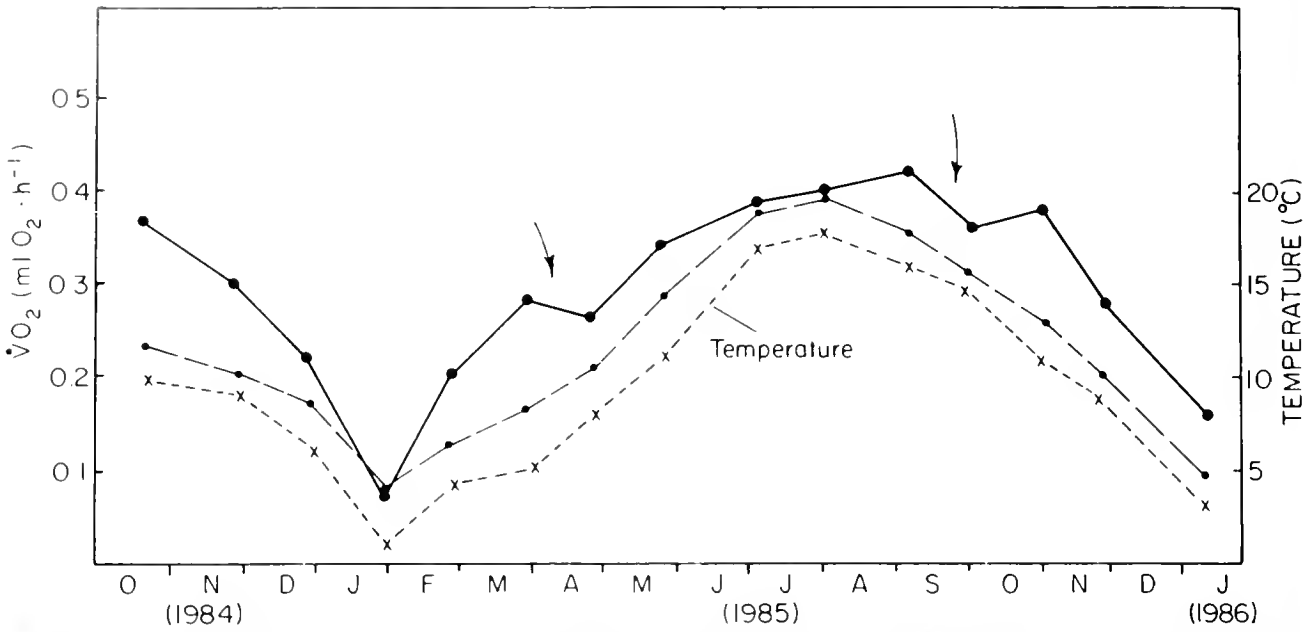

Figure 2. Seasonal changes in oxygen consumption of *Placopecten magellanicus*. (●——●) represents measured $\dot{V}O_2$ (●– – –●) expected rates of $\dot{V}O_2$ based on acclimation data (see Figure 1) and the environmental temperatures (x– – –x). Data presented are for a standard animal of 1g dry tissue weight.

Seasonal changes in metabolic rate reflect the various interactions between food availability, temperature, growth and reproductive activities. *P. magellanicus*, like other scallops (Mason, 1958; Ansell, 1974; Comely, 1974; Barber and Blake, 1981, 1983), exhibits a distinct annual reproductive cycle and as shown in Figure 3, the gametogenic cycle and energy utilization are intimately related. This in turn affects metabolic rate (see Barber and Blake, 1985).

Previous authors have studied the pattern of gonad development in *P. magellanicus* from various areas with contrasting results. Thompson (1977) showed that reproductive development in Newfoundland begins in spring and the gonads mature in the summer. He further showed that energy reserves from the previous year played no part in gonadal development. In contrast, Robinson et al. (1981) found that gametogenesis began in December/January in animals from Boothbay Harbor, Maine and that gonad de-

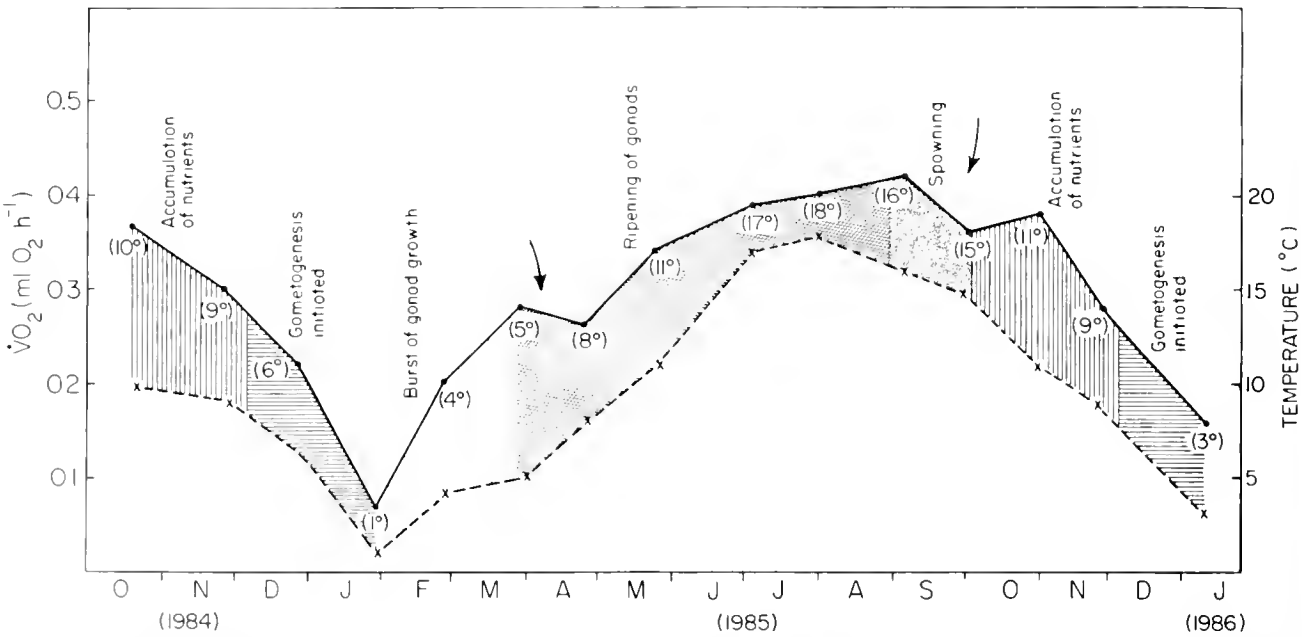

Figure 3. Seasonal changes in oxygen consumption of *Placopecten magellanicus* (from Figure 2) and approximate periods of the gametogenic cycle in the Gulf of Maine.

velopment takes place during January-March concurrently with somatic tissue growth. The energy reserves in the somatic tissues were lost in late spring-summer after the maturation of the gametes, i.e. energy for gametogenesis comes from both the stored reserves and from the ingested ration unlike the more northern populations in Newfoundland where energy reserves from the previous year play no part in gonadal development.

The gametogenic cycle for *P. magellanicus* from Maine can be summarized as follows: During January, gametogenesis has already reached the early developmental stage; energy reserves are at their lowest level (Robinson et al., 1981), and energy must be mobilized from the accumulated reserves. During the spring, gametogenesis is underway, gonad size increases, feeding begins with coincidental spring phytoplankton blooms and energy reserves begin to accumulate. During the summer (June–August), food is plentiful, gametes are ripening and energy is derived from spring storage and from food intake (Robinson et al., 1981). Spawning takes place in September/October and the animals enter a reproductively quiescent or 'rest' period. Barber et al. (1988) found that primary oogenesis was initiated in February, secondary oogenesis in March and vitellogenesis after June in *P. magellanicus* from Boothbay Harbor, Maine. Spawning and resorption of mature ova was evident in September and to a greater extent in October after which the animals were in a period of recovery (December/January).

In the present study, we have shown that respiration rates of *P. magellanicus* exhibited pronounced seasonal fluctuations which generally followed the changes in environmental temperature. While seasonal changes in metabolic activity are probably more closely related to food supply or reproductive activity than to temperature *per se*, in *P. magellanicus* there is a strong relationship between environmental temperature and seasonal changes in metabolic rate. These results are in general agreement with those of MacDonald and Thompson (1986a,b). Highest rates are exhibited during the summer months (ripening of the gonads) and lowest rates are exhibited during the winter months when gametogenesis is initiated.

It is demonstrated here that seasonal variations in metabolic rate are intimately linked with the gametogenetic cycle as has been demonstrated for several other species of molluscs (see Bayne and Newell 1983 for review). This cycle is not strictly related to temperature. During the spring and summer months, glycogen is stored and during the autumn and winter months this energy store is utilized for metabolism (including gametogenesis, see Gabbott, 1975). In scallops, glycogen stored in the adductor muscle is the major energy substrate (Ansell, 1974; Barber and Blake, 1981; Robinson et al., 1981).

The greatest discrepancy between the observed rates of respiration and those expected based on Q_{10} values occurred during February and March when there was a sudden increase in $\dot{V}O_2$ coupled with only a slight increase in environmental temperature. This increase is most likely associated with the increased energy requirements of the scallop to fuel the sudden increase in gonad growth. This further suports the suggestion of Vahl and Sundet (1985) that the attainment of sexual maturity has an energetic cost. The observed $\dot{V}O_2$ from the end of January and the end of March is greater than would be expected based on Q_{10} values. Gonad development is an energy demanding process usually requiring mobilization of nutrients from ingested food or the storage and subsequent utilization of reserves from the body tissues. This period of time may correspond to the period of proliferation of the gonad/differentiation of gametes which is then followed, between April and August, by the less (?) energetically demanding process of gamete ripening.

The two 'unexpected' decreases in $\dot{V}O_2$ observed during March/April and August/September are of particular interest (see Figures 2,3). Similar decreases have been seen previously for this and other species. Ehinger (1978) concluded that reproductive stage had no effect on the rate of respiration. Closer examination of her data, however, reveals that the trends in her study were similar to those reported here and in fact, the same decrease after spawning is reported in her thesis. Bricelj et al. (1987) noted a similar decrease in $\dot{V}O_2$ after spawning in *A. irradians*. Barber and Blake (1985) reported a similar decrease in $\dot{V}O_2$ between mid- and late June (temperatures virtually the same) at about the time cytoplasmic growth of oocytes was initiated in *A. irradians* from Florida. He also noted a concomitant increase in RQ and O/N ratio both indicative of a shift toward greater carbohydrate utilization. March/April is the period of secondary oogenesis in *P. magellanicus* (Barber et al., 1988). It is possible that the initial decrease in $\dot{V}O_2$ observed in early spring by Barber and seen in this study is the result of the invocation of this metabolic machinery. The second decrease, corresponding to spawning, is accompanied in bay scallops by a shift from carbohydrate catabolism to protein catabolism (Barber and Blake 1985) and similar mechanisms are probably in effect in *P. magellanicus*

It is difficult to separate the effect(s) of food, temperature and reproductive stage on metabolic rate because they all vary simultaneously. Only when we have a clear knowledge of the seasonal changes in food availability and feeding strategies in this species can the allocation of energy between somatic and gametogenic growth be clearly understood.

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BIOLOGICAL FEASIBILITY OF GROWING THE NORTHERN BAY SCALLOP, *ARGOPECTEN IRRADIANS IRRADIANS* (LAMARCK, 1819), IN COASTAL WATERS OF GEORGIA

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ABSTRACT Two studies were carried out to evaluate the potential of pearl net cultivation of non-native (northern) Bay Scallops, *Argopecten irradians irradians* (Lamarck, 1819), in the coastal waters of Georgia. In October 1984, scallops ($\bar{x}$ = 9.8 mm ± 0.21 S.E.) were placed in pearl nets suspended from a floating raft in House Creek, Little Tybee Island, Georgia, at a density of 70/net. By May 1985, scallops averaged 43.2 mm ± 2.3 S.E. in shell length with 27% larger than 50 mm (commercial size) and 47% survival. In a second study (October 1985–June 1986), density dependent and site specific effects on scallop (initial size = 6.5 mm ± 0.1 S.E.) growth were evaluated between an "exposed" site (Priest Landing) and a "sheltered" site (House Creek). Growth at the "sheltered" site was significantly greater at similar stocking densities (100/net; 200/net) and also at higher stocking densities than at the "exposed" site. By June 1986, the House Creek 100/net treatment showed mean shell length of 37.6 mm with 68.2% survival. At 200/net mean shell length was 37.9 mm with 48.5% survival. At the exposed site, growth was significantly greater in nets placed <0.3 m below the surface ($\bar{x}$ = 36.0 mm at 100/net) as opposed to nets at greater depths (3 m) ($\bar{x}$ = 33.3 mm at 100/net and 32.2 mm at 200/net). Survival rates at Priest Landing ranged from 36.5 to 64.2% in June 1986. None of the scallops in the 1985–86 experiments had reached market size by June. These results show that non-native Bay Scallops can grow and survive in the coastal waters of Georgia with acceptable survival between October and May–early June.

Although smaller northern bay scallop seed (*ca.* 10 mm) can grow to a minimal commercial size with acceptable survival when grown from fall to spring in the coastal waters of Georgia, it is doubtful that this subspecies has a maricultural future for Georgia fishermen. To ensure adequate growth and survival, nets must be cleaned monthly to control fouling organisms. This constant cleaning process and the fact that scallops only grow to a minimal marketable size will prevent the farming of this subspecies in coastal Georgia.

KEY WORDS: Scallop mariculture, *Argopecten irradians*, pearl net cultivation

INTRODUCTION

The bay scallop, *Argopecten irradians irradians* (Lamarck 1819), is an important commercial species of scallop along the Atlantic and Gulf coasts of the United States, with the fishery centered in the New England states and on the Gulf coast of Florida. In 1985, 0.735 million pounds of scallop meat were landed in the United States (National Marine Fisheries Service 1986). During peak season in 1985, bay scallops from northern areas (Long Island and Massachusetts) fetched $6.66/lb. while those from North Carolina commanded $5.69/lb., according to the green sheet (New York market reports). Dockside values of $3.50/lb. were common during peak season while a 35% price reduction occurred during the marketing of the calico scallop harvest (anonymous reviewer).

Due to its commercial and ecological significance, the bay scallop has traditionally received a lot of attention from researchers. While only those works with direct relevance to the present study are cited herein, the readers are referred to the excellent reviews of bay scallop literature contained in the works of Broom (1976), Robert (1978), and Fay et al. (1983).

The distribution of the bay scallop ranges from New England to the Gulf of Mexico (Abbott 1974), primarily in protected bays where seagrasses or seaweeds provide a natural refuge for the animal (Dreyer and Castle 1941; Thayer and Stuart 1974; Orth 1977; Stoner 1980; Eckman 1987). *Argopecten irradians* (Lamarck 1819) is divided into two subspecies: *Argopecten irradians irradians* (Lamarck 1819) which occurs from Cape Cod to New Jersey and *Argopecten irradians concentricus* (Say 1822) which occurs from Maryland to Georgia and Louisiana to Tampa, Florida (Abbott 1974). Although Georgia has approximately ⅓ of the salt marsh acreage along the Atlantic coast, bay scallops do not occur there, probably due to the lack of submerged vegetation (personal observations). The absence of the bay scallop is regrettable since it is an ideal species which commands high prices (Castagna and Duggan 1971a, 1971b).

The life span of the bay scallop is 1.5 to slightly over 2 years (Marshall 1963; Taylor and Capuzzo 1983). The time required for bay scallops to reach marketable size (50 mm) decreases with decrease in latitudes (Castagna and Duggan 1971b). Hard clams, *Mercenaria mercenaria* (L.), from natural populations in coastal Georgia obtain marketable size in 2 to 3 years (Walker 1987); whereas, 4 to 5 years of growth are required in the Long Island Sound, New York area (Greene 1978). Northern hard clam seed ($\bar{x}$ = 6 mm in shell length) obtained marketable size in 18 months

when grown in the coastal waters of Georgia (Walker 1984). Thus, it may be possible that growth to a marketable size for the northern bay scallops might take less time in the warmer Georgia waters than in their native northern waters.

As part of an ongoing Mariculture Development Program at the University of Georgia, a wide variety of potential mariculture species are being studied. The initial investigation involves testing the biological feasibility of the species in coastal Georgia. If this is deemed acceptable, an economic feasibility study is then conducted.

The purpose of the research reported here was to determine if the northern bay scallop, a non-native species, can grow and survive in the coastal waters of Georgia, and to evaluate the potential fishery that might be developed for this species in Georgia. Ease of access to seed of northern bay scallops dictated that they be investigated at this stage in preference to the southern bay scallop whose seed is not readily available.

MATERIAL AND METHODS

1984–1985 Experiment at House Creek:

Bay scallops were obtained from Bristol Shellfish Farms, Round Point, Maine. They were set up at a mean shell length of 9.8 mm ± 0.2 S.E. in 11 pearl nets (0.3 × 0.3 m) suspended (0.3 m depth) from a floating raft at a density of 70/net on 21 October 1984. The raft was anchored within a small tidal creek at Little Tybee Island (Figure 1). The nets were checked monthly, cleaned of fouling organisms and the shell length of at least 200 scallops (except for October and November) was measured using vernier calipers. There were a considerable number

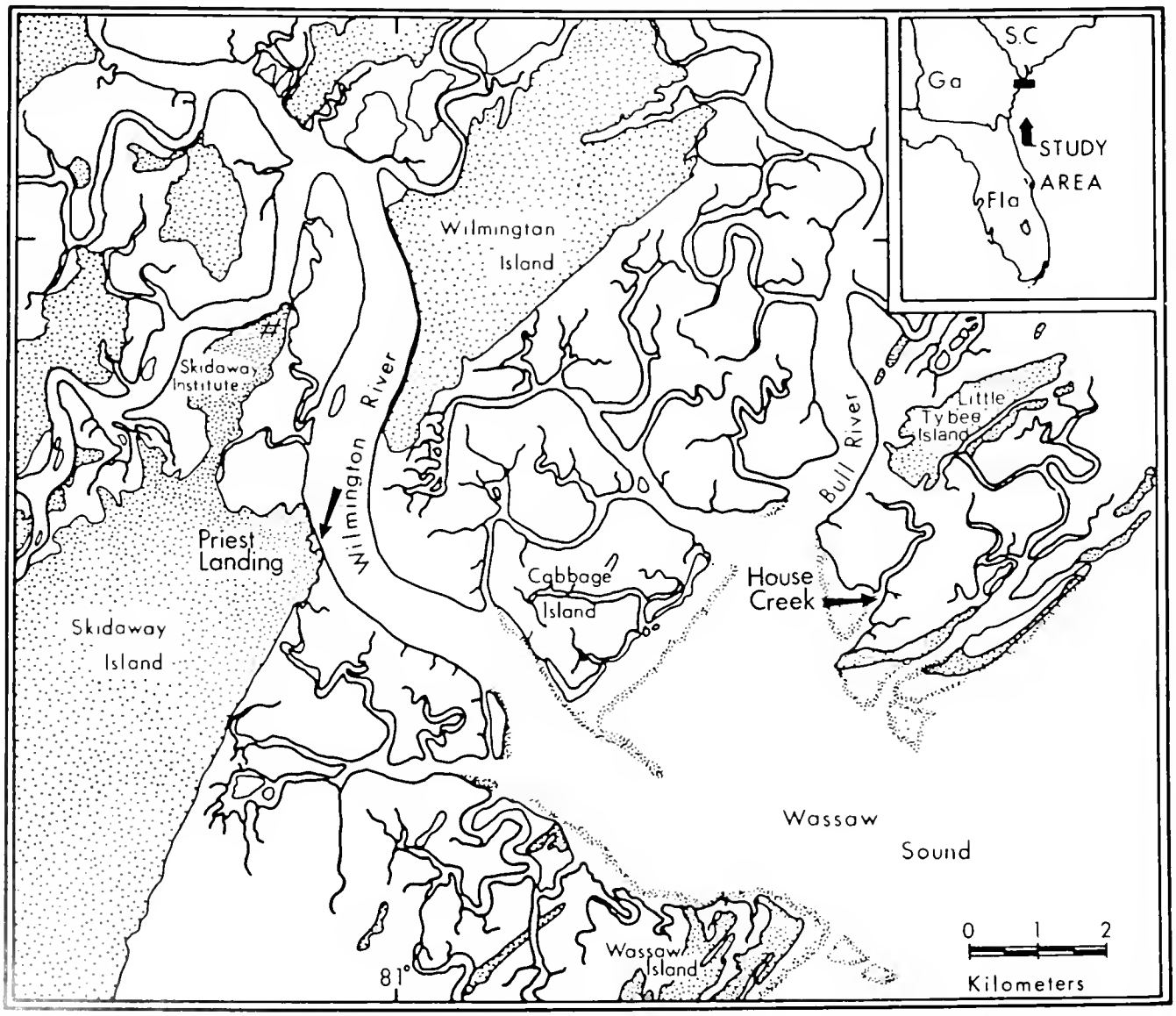

Figure 1. Map of the study area indicating the exposed (Priest Landing) and sheltered (House Creek) sites in which pearl net cultivation of *Argopecten irradians irradians* was carried out.

of deformed seed present from the onset of the study (see Results).

1985–1986 Experiment at House Creek and Priest Landing:

Scallops were shipped from the Aquaculture Research Corporation, Dennis, Massachusetts. They were set up in density replicates (100/net and 200/net) in pearl nets (0.3 × 0.3 m) suspended (0.3 m depth) from floating rafts at Priest Landing and House Creek on 9 October 1985 at a mean shell length of 6.5 mm ± 0.1 S.E. The Priest Landing experiment also contained a trial designed to evaluate the effect of depth on growth, with a suite of nets (n = 6; 3 at 100/net, 3 at 200/net) suspended *ca.* 0.3 m below the surface and another at *ca.* 3 m depth (n = 6; 3 at 100/net and 3 at 200/net). House Creek replicates (n = 12; 5 at 100/net and 7 at 200/net) were all at a depth *ca.* 0.3 m.

Nets were examined, with total counts and measurements of all scallops carried out on January 14–15, March 30–April 1 and June 4–5, 1986. Fouling organisms were removed and/or nets were replaced during each sampling season. Results were compared statistically using student t-tests (at 95% confidence level).

RESULTS

1984–1985 Experiment at House Creek:

From 21 October 1984 to 13 June 1985 scallops grew from a mean shell length of 9.8 ± 0.2 mm to 49.0 ± 3.4 mm in pearl nets suspended from a floating raft (Table 1 and Figure 2). Although scallop growth slowed during January and February, it was continuous throughout the study period. Large sample errors were due to difference in individual growth rates and shell deformities. For instance, in April scallops without deformities ranged from 12.9 mm to 61.6 mm in shell length ($\bar{x}$ = 43.3 ± 0.6 mm). Deformed scallops, accounting for 21% of the animals sampled, ranged from 12.9 to 54.6 mm in shell length ($\bar{x}$ = 23.8 ± 0.9 mm).

By June 13, 1985, only 3% of the scallops remained alive. Water temperatures rose from 26°C (June 1) to 29.7°C during a heat wave in the first week of June. By June 13, water temperatures dropped to 25°C (as recorded at the Marine Extension Service Skidaway Island dock). However, on May 16, survival was at 47%, with a mean shell length value at 43.3 mm (±2.3) (Figure 2). By this time, 27% of the scallops sampled were marketable size (Table 1). The daily growth rate from October 21 to May 26 (206 days) was 0.162 mm/day.

1985–1986 Experiments at House Creek and Priest Landing:

By January 1986, site specific significant differences were evident between treatments at Priest Landing and House Creek. Scallop growth was significantly greater in the House Creek 100/net (H100) treatment ($\bar{x}$ = 24.9 mm) than in the "surface" (<0.3 m depth) treatment with 100/net at Priest Landing (PS100) ($\bar{x}$ = 20.9 mm) (see Tables 2 and 3). There were no significant differences in growth between other House Creek and Priest Landing treatments by January. There were no density dependent significant differences in growth between House Creek treatments. Priest Landing 200/net "bottom" (*ca.* 3 m depth) treatment PB200 ($\bar{x}$ = 23.2 mm) and the 100/net "bottom" (PB100) ($\bar{x}$ = 24.8 mm) treatment both displayed significantly greater growth than the surface treatment (PS100, $\bar{x}$ = 20.9 mm) (Table 2). Mean survival rates were all greater than 90% (90.8–98.8%) during January (see Figure 3).

By March 31–April 1 there were site specific and density dependent significant differences in growth rates observed between the various treatments. The House Creek treatments were significantly greater in mean size than their counterparts at Priest Landing, e.g., H100 ($\bar{x}$ = 36.1 mm) > PB100 ($\bar{x}$ = 29.1 mm) > PS100 ($\bar{x}$ = 28.9 mm) and H200 ($\bar{x}$ = 32.9 mm) > PB200 ($\bar{x}$ = 26.7 mm) (Tables 2 and 3, Figure 2). The H200 treatment was also significantly greater in mean size than the PB100 and PS100 treatments.

TABLE 1.

Growth of Bay Scallops, *Argopecten irradians irradians*, in the coastal waters of Georgia.

Date	Number of Scallops measured for shell length	Shell Length in mm ± S.E.	Percentage of Scallops >50 mm	Percentage Survival
21 October 1984	57	9.8 ± 0.2	0	—
17 November 1984	59	14.0 ± 0.7	0	—
9 December 1984	272	24.7 ± 0.5	0	—
18 January 1985	368	34.4 ± 1.8	0.3	—
18 February 1985	257	38.6 ± 2.4	7.8	—
18 March 1985	477*	37.7 ± 1.7	15.9	62.0
18 April 1985	462*	39.0 ± 1.8	21.4	60.0
13 May 1985	361*	43.3 ± 2.3	26.6	47.0
13 June 1985	24*	49.0 ± 3.4	56.0	3.1

* Total count and measurement of scallops from all pearl nets.

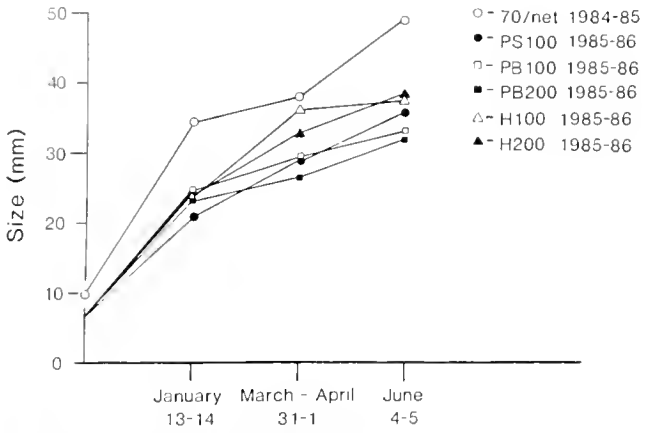

Figure 2. Growth of *Argopecten irradians irradians* in various density treatments during October–June 1984–85 and 1985–86. PS = Priest Landing Surface (0.3 m), PB = Priest Landing Bottom (*ca.* 3 m), H = House Creek, e.g. H100 = House Creek 100/net etc.

Density dependent significant differences in growth were observed at House Creek, with H100 greater than H200 (see Table 3). Similarly PB100 was significantly greater than PB200 in observed growth while the differences between PS100 and PB100 were not significant. Survival rates ranged from 69.3% (PB200) to 87% (PB100) on March 31–April 1 (see Figure 3).

At the termination of the study on June 4–5, 1986 the mean growth of the House Creek treatments was significantly greater than any of the Priest Landing treatments (see Tables 2 and 3). Mean sizes at House Creek varied from 34.4 mm–40.1 mm (H100) and 35–40.9 mm (H200) while those at Priest Landing ranged from 32.2 mm (PB200) to 33.8 mm (PB100) and 34–37.7 mm (PS100) (Tables 2 and 3). There were no density dependent significant differences in scallop growth among treatments at House Creek or on the bottom at Priest Landing (i.e., PB100 and PB200). The surface treatment at Priest Landing (PS100, $\bar{x}$ = 36.0 mm) showed significantly greater growth than the bottom treatment (PB100, $\bar{x}$ = 33.3 mm) (see Figure 2). Survival rates by 4–5 June varied from 36.5% (PB100) to 68.2% (H100). Daily growth rates over the study period (238 and 239 days at Priest Landing and House Creek, respectively) are presented in Table 4. The H200 treatment exhibited the fastest growth rate with 0.132 mm being added to shell length daily (Table 4).

The observed bay scallop growth rates are not sufficient to support this species as a good mariculture candidate for Georgia. Furthermore, the labor intense nature of pearl net cultivation for bay scallops will also rule out this grow-out system for mariculturists in Georgia.

DISCUSSION

The results presented here show that bay scallops can survive and be grown to a minimum commercial size in the coastal waters of Georgia. The growth rates reported here are comparable to those published from other areas of the eastern U.S. In Georgia scallops grew from 9.8 mm to 49 mm (1984/5) and from 6.5 mm to 33.3–37.9 mm (1985/6) in *ca.* 8 months. In Massachusetts, 12 to 17 months are required for scallops to reach 50 mm (Belding 1910), whereas, in North Carolina, 10 months are required (Gutsell 1928). In Virginia seed scallops grew from 12.7 mm to 57 mm in 6 to 7 months (Castagna and Duggan 1971a) and from 14.4 mm to 47 mm in 4 months (Duggan 1973). However, growth patterns are quite different in Georgia than in northern states. Growth in Georgia was continuous throughout the winter months (Figure 2), whereas growth frequently ceases during this period in northern states, e.g., scallop growth stops below 7°C in Massachusetts (Belding 1910). Since 1958 Georgia coastal water temperatures have dropped below 7°C during only 10 winters, with the

TABLE 2.

***Argopecten irradians irradians* pearl net growth experiments at Priest Landing October 1985—June 1986.**

Initial Density	9 October Size (mm) (±S.E.)	15 January 86 Size (±S.E.)	% Surv.	1 April 86 Size (±S.E.)	% Surv.	5 June 86 Size (±S.E.)	% Surv.
Surface (<0.3 m)							
100	6.5 ± 0.1	21.1 ± 0.9	100	31.3 ± 1.0	87	37.7 ± 0.9	70
100	6.5 ± 0.1	19.7 ± 0.8	59	29.3 ± 1.0	55	35.5 ± 1.1	49
100	6.5 ± 0.1	19.4 ± 1.4	99	29.1 ± 0.9	87	35.0 ± 0.8	70
100	6.5 ± 0.1	22.7 ± 1.2	100	30.2 ± 0.8	97	37.7 ± 0.9	72
100	6.5 ± 0.1	21.7 ± 1.2	96	21.4 ± 0.6	66	34.0 ± 0.8	60
100	6.5 ± 0.1	Lost	—	—	—	—	—
Subtidal							
100	6.5 ± 0.1	24.8 ± 1.0	93	29.2 ± 0.7	100	32.3 ± 0.9	27
100	6.5 ± 0.1	24.1 ± 1.2	97	28.0 ± 0.7	77	33.8 ± 0.7	46
100	6.5 ± 0.1	25.7 ± 1.4	89	29.3 ± 0.7	84	Lost	
200	6.5 ± 0.1	23.7 ± 1.1	98.5	26.2 ± 0.5	62.5	32.2 ± 0.5	58
200	6.5 ± 0.1	22.7 ± 1.0	98	26.9 ± 0.5	84.5	Lost	
200	6.5 ± 0.1	23.1 ± 0.8	100	26.6 ± 0.5	61	Lost	

TABLE 3.

Argopecten irradians irradians pearl net growth experiments at House Creek October 1985–June 1986. (All subtidal).

Initial Density	9 October 85 Size (mm) (±S.E.)	14 January 86 Size (mm) (±S.E.)	% Surv.	1 April 86 Size (mm) (±S.E.)	% Surv.	5 June 86 Size (mm) (±S.E.)	% Surv.
100	6.5 ± 0.1	26.4 ± 0.8	97	35.7 ± 1.0	90	40.1 ± 0.5	78
100	6.5 ± 0.1	22.9 ± 0.9	100	35.3 ± 0.9	97	38.7 ± 0.7	73
100	6.5 ± 0.1	24.4 ± 0.9	100	38.6 ± 0.9	40	38.4 ± 1.0	51
100	6.5 ± 0.1	26.8 ± 0.8	93	36.1 ± 0.8	85	36.9 ± 0.6	68
100	6.5 ± 0.1	24.0 ± 1.0	96	35.2 ± 1.0	?	34.4 ± 0.7	71
200	6.5 ± 0.1	23.5 ± 1.0	86	34.4 ± 1.0	65.5	40.9 ± 0.6	43
200	6.5 ± 0.1	26.4 ± 1.0	97.5	34.6 ± 1.0	77	37.8 ± 0.6	45.5
200	6.5 ± 0.1	25.1 ± 0.8	97	31.2 ± 0.9	78.5	39.0 ± 0.6	43.5
200	6.5 ± 0.1	22.4 ± 0.8	99	32.7 ± 1.0	71.5	38.9 ± 0.7	43
200	6.5 ± 0.1	24.5 ± 0.8	97.5	Lost	—	—	—
200	6.5 ± 0.1	22.9 ± 0.7	90.5	31.3 ± 1.1	82.5	35.0 ± 0.5	67.5
200	6.5 ± 0.1	24.7 ± 0.7	97.5	Lost	—	—	—

"drop" in temperatures usually of less than 1-week's duration.

The two experiments reported here indicate commercially acceptable survival rates (i.e., 47–68%) using pearl net cultivation as long as northern bay scallop harvesting is completed before lethal water temperatures (*ca.* 26°C) are reached in June. As demonstrated in June 1985, very high mortalities occur at water temperatures in excess of 26°C.

Site characteristics have been shown to have a profound effect on the growth of scallops during this study. The sheltered creek site (House Creek) exhibited significantly greater scallop growth rates than the exposed site (Priest Landing). The creek location obviously afforded a lot of shelter from natural elements as well as commercial and recreational boat traffic disturbances, with consequent beneficial effects on observed growth rates. This is in agreement with the findings of Kirby-Smith (1972), where a fast water-flow rate was shown to adversely affect bay scallop growth. The raft with scallops at House Creek sits in a pool of water (0.6 to 1 m deep) at low tide. Most of the creek is drained at low tide while scallops at Priest Landing are anchored in a major river with 6 meters of water below the raft at low tide. In the absence of water temperature and current velocity data pertaining to the two sites, one can only speculate that temperatures fluctuated greater in the shallower sheltered creek and water movement was higher at the exposed site on Wilmington River. The significantly superior growth of scallops in the exposed sites "surface" treatment as opposed to the "bottom" treatment contrasts with the findings of Duggan (1973), where growth was equal throughout the water column. The higher mortalities suffered in the "bottom" nets agrees with the results of Duggan (1973). The lower growth and survival of scallops reared in "bottom" pearl nets may be related to varying pressures exerted by fouling organisms. The "surface" nets were fouled mainly by *Molgula* (sea squirt), oyster spat, barnacles and branching bryozoans while the "bottom" nets were predominantly fouled by encrusting bryozoans. There was no clear relationship between survival and site selection and/or density treatments.

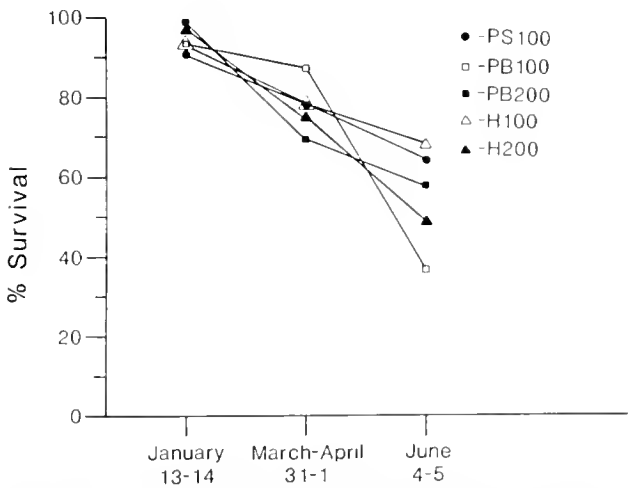

Figure 3. Mean survival rates for *Argopecten irradians irradians* pearl net cultivation experiments at Priest Landing and House Creek October 1985–June 1986. PS = Priest Landing Surface, PB = Priest Landing Bottom, H = House Creek, e.g. H100 = House Creek 100/net.

TABLE 4.

Mean daily growth rates for *Argopecten irradians irradians* reaed in pearl nets in two sites in coastal Georgia October 1985–June 1986.

Site/Density	Growth Rate mm/day
Priest Landing (Exposed)	
100/net (Surface)	0.124
100/net (Bottom)	0.112
200/net (Bottom)	0.108
House Creek (Sheltered)	
100/net (Bottom)	0.130
200/net (Bottom)	0.132

Growth rates of northern bay scallops cultivated in pearl nets during periods of amicable water temperatures in coastal Georgia do not suggest a bright future for this grow-out system for the southern mariculturist. The observed growth rates (0.162 mm/day) at a stocking density of 70/net (9.8 mm seed) yielded barely minimum commercial size scallops within a 206 day growing season. Use of larger seed (15–25 mm) and lower initial stocking densities (30–70/net) could yield bigger scallops, but the extra cost of larger seed and additional nets may be offsetting. Furthermore, the labor input necessary to maintain relatively unfouled nets in open seawater systems may prove prohibitive for any commercial undertaking in Georgia. Considerable attention is currently being devoted to the interstate movement of shellfish by state and federal legislators. Future legislation prohibiting and/or limiting the movement of shellfish resources due to the threat of disease, is a distinct possibility. Such prohibitive legislation could rule out such overwintering programs as those discussed here.

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BACTERIAL DEPURATION BY THE HARD CLAM, *MERCENARIA MERCENARIA*

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ABSTRACT Bacterial loads varied in hard clams obtained from a South Carolina estuary with lower counts during cooler months and higher counts during warmer months; the water source from which clams were taken was considered unpolluted as low levels of fecal coliforms and no *Salmonella* or *Shigella* spp. were detected. *Vibrio parahaemolyticus* was detected only in low numbers in hard clams. Two important parameters considered in depuration were salinity and temperature. Clams raised in South Carolina coastal waters provided good depuration results within 24 h at a temperature close to 24°C and salinities of 24–31‰. No apparent "thermal shock" was observed when clams were depurated at higher than ambient temperatures; "cold shock" was observed when clams acclimated at higher temperatures were depurated at lower temperatures. Clams preloaded with bacteria at 30°C (salinity of 26.5‰) required 24–48 h of depuration at 20°C.

KEY WORDS: Bacterial depuration, hard clam, *Mercenaria mercenaria*

INTRODUCTION

The hard clam, *Mercenaria mercenaria*, is a natural resource along the South Carolina coast. However, the availability of edible shellfish throughout the year is dependent upon the bacterial content of their environment and of the mollusks themselves. Along the coast of South Carolina, sewage outfalls are major sources of pollution; an increase in summer visitors also presents a public health problem as waste disposal needs increase. High coliform counts, indicative of sewage pollution, may be attributed to storm water run-off from residential areas and shopping mall parking lots, livestock, domestic fowl, migratory water fowl and/or heavy rains which contribute to overloaded sewage treatment facilities. As the temperature increases during warmer months, total bacterial content and fecal coliform counts increase. Once fecal coliform levels rise above the guidelines set forth by the National Shellfish Sanitation Program (NSSP), the shellfish are no longer safe for human consumption. At this time, a major resource and food source is unavailable.

Shellfish purification has been studied for clams (Cantelmo and Carter 1984, Hartland and Timoney 1979, MacMillan and Redman 1971, Ritchie 1976, and Timoney and Abston 1984), oysters (Eyles and Davey 1984, Huntley and Hammerstrom 1971, Janssen 1974, and Rowse and Fleet 1984) and mussels (Houser 1964 and Ledo *et al.* 1983) and is a viable alternative for using mollusks that have been exposed to polluted waters. These reports suggest that site-specific studies would be required to determine optimal conditions for depuration of bacteria by shellfish. The present study was undertaken to examine specific parameters (salinity and temperature) necessary for depuration of bacteria from clams growing in coastal waters of South Carolina, and to determine levels of sewage pollution and indigenous bacteria in clams from an unpolluted estuary in South Carolina.

MATERIALS AND METHODS

Collection and Mointenance of Shellfish

Hard clams (*Mercenaria mercenaria*) were obtained from Trident Sea Farms of Charleston, South Carolina and transported to the Waddell Mariculture Center at Bluffton, South Carolina. The basic grade (size) of clams used was the little neck with some cherrystones. Clams averaged 50.0 mm in length with a size range of 38–74 mm. Clams were maintained in a fiberglass tank supplied with a flow-through water system of sand-filtered seawater. Water was obtained from the Colleton River Estuary. Clams used for depuration studies at Clemson University were shipped in styrofoam containers with ice, packed so as not to directly contact the clams. After arriving at Clemson University, the clams were placed in tanks (22 l) containing artificial seawater (ASW; Rila Marine Mix, Rila Product Company, Teaneck, New Jersey) at 26.5‰ and 25°C. Water was aerated and circulated using a commercial aquarium pump. Clams were fed a variable amount of algal suspension of *Isochrysis galbana* and *Chaetoceros gracilis* (cell density, 10^3/ml) at 3-day intervals. Three days prior to each experimental study, clams were placed in a tank (22 l) containing fresh artificial seawater at 26.5‰ at 25°C and allowed to pump without feeding.

Bacterium

A chloramphenicol resistant strain of *Escherichia coli* was obtained by mutating a parental strain (ATCC 25922) with ultraviolet light. The mutant was cultivated at 37°C for 18 h in Brain Heart Infusion (BHI) broth (Difco Lab) or at 37°C on BHI agar medium (Difco Lab) to which filter sterilized (0.45 μm; Gelman Acrodisc) chloramphenicol (Sigma Chemical Company) was added to a final concentration of 100 μg/ml.

Loading

Clams were initially scrubbed with a stiff bristled brush under running potable water to remove debris from their shells. They were then placed in a plastic container, covered with damp paper towels, and placed in a 4°C room for 24 h and then at 25°C for 12 h. This procedure facilitated uptake (personal communication, John Manzi) of bacteria by clams. A pre-loading sample of three to five clams was removed for processing to determine the initial bacterial concentration. Groups of 36 clams were then evenly separated in tanks (22 l) containing ASW, at 26.5‰, and a temperature of 25°C. The water was aerated and circulated using a commercial aquarium pump. Clams were exposed for 4 h to chloramphenicol resistant *E. coli* (approximately 5×10^4 per ml), removed from the contaminated water, placed in wire baskets and scrubbed with a stiff-bristled brush under potable running water. Only those clams that were observed to have extended siphons during loading were measured and used for depuration studies. The percentage of clams that siphoned was recorded.

Depuration Studies

Clams preloaded with bacteria were placed in tanks (22 l) containing clean seawater as previously described. Zero h was recorded at the moment shellfish were placed into experimental tanks. Clam samples were removed at 0, 4, 8, 12 and 24 h intervals. Seawater salinity and temperature were monitored for their effect on shellfish depuration. Temperature was controlled by placing experimental tanks into temperature controlled chambers (Scientific Systems). A synthetic seawater mix (Rila Marine Salts) was used to prepare water at different salinities.

Processing of Shellfish

Samples of three or more clams were washed and scrubbed with a stiff-bristled brush under running potable water, air dried and measured before being aseptically shucked into a sterile tared beaker. Clam meat and liquor were weighed to the nearest gram and transferred to a sterile blender (Waring). To each sample, sterile 0.2 M phosphate buffer, pH 7.6, was added to dilute the sample 1:4 (w/v) and blended for 30 s at low speed, then for 60 s at high speed. Four milliliters of homogenate contained approximately 1 g of clam meat and liquor.

Tenfold serial dilutions of homogenate were made to the 10^{-4} dilution, using sterile 0.2 M phosphate buffer (pH 7.6). Samples were spread-plated, in duplicate, with 0.1 ml of serially diluted clam homogenate on BHI agar medium supplemented with chloramphenical (100 μg/ml). Plates were incubated at 37°C and colony forming units were counted after 24 h.

Temperature Shift Studies

Collection of shellfish, bacterium used, and loading procedures were as previously described. Maintenance of shellfish was altered; after arrival at Clemson University, clams were divided evenly into three groups and placed in three tanks (22 l each) containing ASW at 26.5‰ and water temperatures of 20° or 30°C. Clams preloaded with bacteria were placed in tanks as follows: one-half of the clams loaded at 20°C were placed in a tank of 26.5‰ ASW at 30°C, the other half in a tank of 26.5‰ ASW at 20°C; the clams loaded at 30°C were placed in a tank of 26.5‰ ASW at 20°C. Zero time for each experiment was the moment shellfish were placed into tanks. Clam samples were removed at 24 and 48 h intervals for depuration measurements. Temperature was controlled by placing experimental tanks into temperature controlled chambers (Scientific Systems). Processing of shellfish was as described previously.

In situ Bacterial Levels in Clams

Clams (*Mercenaria mercenaria*) were obtained at approximately 2-month intervals from an unpolluted source in the Colleton River Estuary near the Waddell Mariculture Center at Bluffton, South Carolina. Clams were processed within 2 h after arrival, as previously described. At least 25 g of clam meat and liquor were used for each sampling. The clams were homogenized and ten-fold serially diluted to the 10^{-4} dilution.

Total plate counts were obtained by mixing 1 ml of diluted clam homogenate into a pour plate containing melted standard methods plate count agar (American Public Health Association 1984). Duplicate plates for each dilution were prepared and incubated at 35°C for 48 h before colony-forming units were counted.

The most probable number (MPN) of fecal coliform bacteria was obtained using the presumptive and complete tests recommended by the American Public Health Association (1984). Four milliliter aliquots of serially diluted clam homogenate were used to inoculate sets of either three or five MPN tubes in the presumptive test.

Salmonella, *Shigella* and *Vibrio* spp. were enumerated using procedures recommended by the American Public Health Association (1984). A 25 g sample of clam meat and liquor was used for estimating each bacterial population.

RESULTS

A survey was taken of the natural bacterial loads in clams that were in the Colleton River Estuary next to the Waddell Mariculture Center (Table 1). Bacterial loads in clams were highest in the September sample (1.5×10^7 cfu/g shucked clam) and lowest in the March sample (5.3×10^2 cfu/g shucked clam). Few fecal coliforms and no *Salmonella* or *Shigella* spp. were detected. *Vibro parahaemolyticus* was detected in low numbers (3–23 bacteria/g clam meat) throughout the year.

The effect of salinity on hard clam depuration was examined for 24 h at 25°C. Results showed that a salinity of

TABLE 1.

Bacterial Survey of Hard Clams in the Colleton River Estuary

Sample Month/Year	Standard Plate Count (CFU/g Shucked Clam)	Fecal Coliforms (MPN/g)	*V. parahaemolyticus*[a] (MPN/g)	*Salmonella*[c] Detected	*Shigella*[c] Detected
March 1985	5.3×10^2	8[a]	23	0	0
April 1985	8.9×10^3	<3[b]	4	0	0
June 1985	7.4×10^4	4[b]	11	0	0
September 1985	1.5×10^7	<3[b]	9	0	0
November 1985	1.9×10^5	<3[a]	5	0	0
January 1986	3.1×10^3	<3[a]	3	0	0

[a] Three tube MPN method.
[b] Five tube MPN method.
[c] Enrichment culture.

25‰ or 30‰ was more favorable than 20‰ for elimination of preloaded chloramphenicol resistant *E. coli* (Figure 1). The salinities showed no statistical difference at 4 and 8 h; at 12 h, depuration at 30‰ was significantly faster than at 20‰; and at 24 h, both 25‰ and 30‰ showed significantly more depuration than that at 20‰. Clams depurated for 24 h at 25°C and salinities of 25‰ and 30‰ had coliform levels well below standard levels (230 coliforms/100 g clam meat) that are acceptable for marketing (NSSP); clams depurated at a salinity of 20‰ were in excess of NSSP guidelines.

The effect of temperature on hard clam depuration during a 24 h period at a salinity of 25‰ was examined (Figure 2). In general, results showed better depuration at 25°C and 30°C than at 20°C and 35°C (Figure 2). During the initial 4–12 h depuration, temperatures of 30° and 35°C showed, for the most part, significantly better depuration; after 12 h, temperatures of 25° and 30°C gave significantly lower bacterial levels. Depuration was slowest at 20°C.

The interaction of temperature and salinity over a 24 h depuration period is shown in Figure 3. The data suggest that depuration best occurs at a temperature between 24–28°C and a salinity between 24–31‰

A temperature-shift study was run to determine the effect of a shift in temperature on depuration (Figure 4). Clams that were initially acclimated to a temperature of 20°C showed similar depuration for the first 24 h whether the temperature was kept at 20°C or shifted-up to 30°C. An

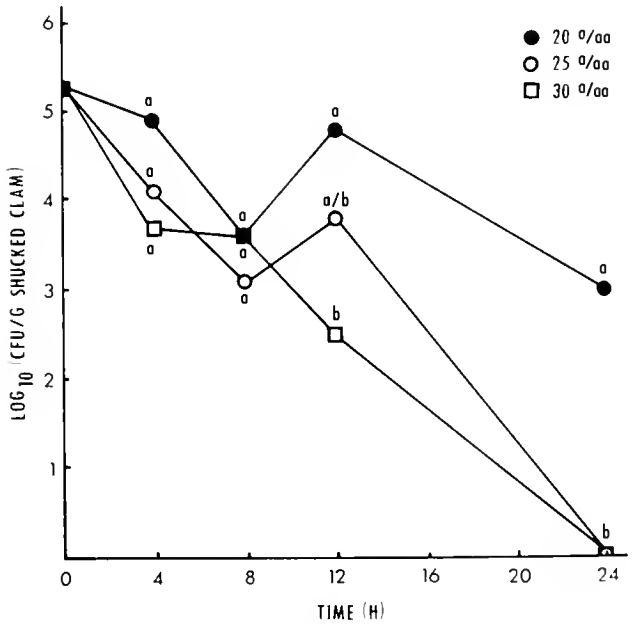

Figure 1. The Effect of Salinity on the Time Course of Depuration of Bacteria (*E. coli*) from Clams (*M. mercenaria*) Incubated at 25°C. Clams were preloaded with *E. coli* at 25°C and 26.5‰ ASW. Data points with different or the same letters at corresponding time intervals are significantly or not significantly different, respectively (analysis of variance, LSD = 0.98 at 0.05 confidence level).

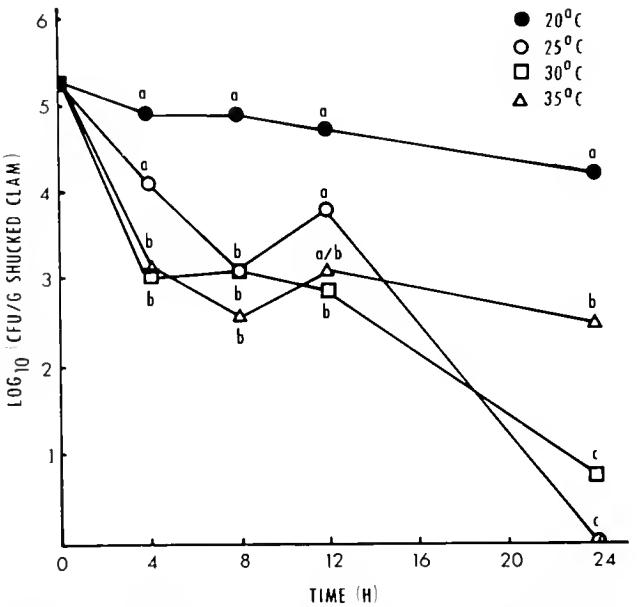

Figure 2. The Effect of Temperature on the Time Course of Depuration of Bacteria (*E. coli*) from Clams (*M. mercenaria*) Suspended in 25‰ ASW. Data points with different or the same letters at corresponding time intervals are significantly or not significantly different, respectively (analysis of variance, LSD = 0.98 at 0.05 confidence level).

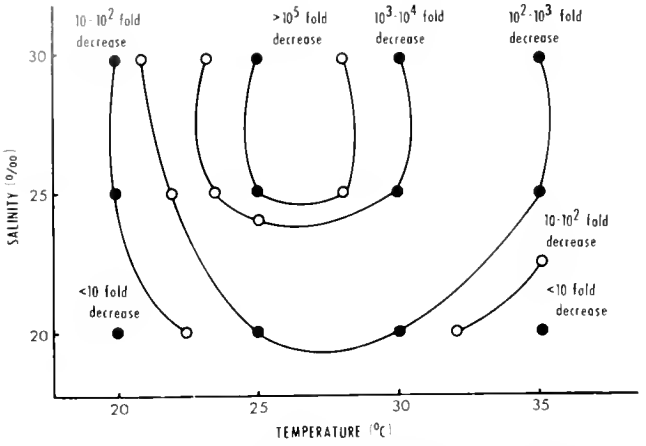

Figure 3. The Effect of Salinity and Temperature on Depuration of Bacteria (*E. coli*) from Clams (*M. mercenaria*). The data represent 10-fold decreases in the number of bacteria in clams after 24 h of depuration. Clams were preloaded with *E. coli* (final concentration: 5 × 10^5 CFU/g shucked clam) at 25°C and 26.5‰ ASW. Experimental data points (●) and extrapolated data points (○) from Figures 1 and 2.

increase in bacterial load in clams depurated for longer than 24 h at 30°C may be attributed to regrowth of *E. coli* and/or resiphoning of previously depurated bacteria. On the other hand, clams acclimated to 30°C and shifted-down to 20°C showed decreased depuration over 24 h. However, their bacterial load was reduced over a 48 h period to a level that was comparable to clams that were not subjected to a temperature-shift (loaded, 20°C/depurated, 20°C).

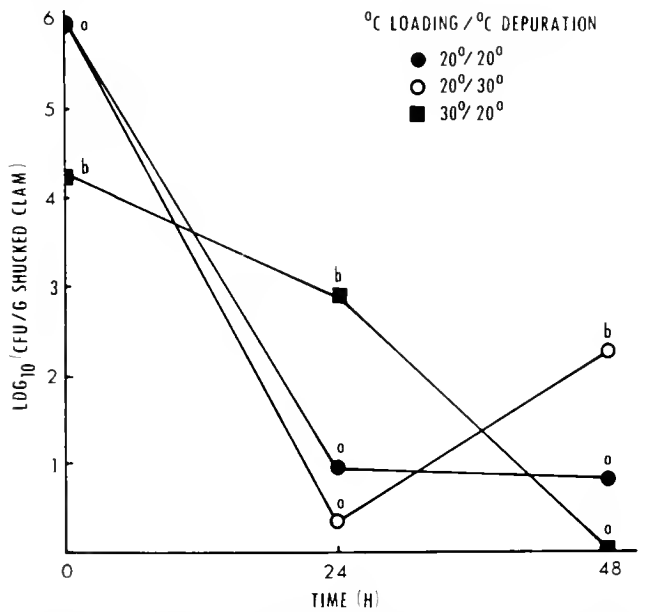

Figure 4. The Effect of a Temperature-Shift on Depuration. Clams were either preloaded with *E. coli* at 20°C and depurated at 20°C or 30°C, or preloaded with *E. coli* at 30°C and depurated at 20°C. The salinity of the experiments was 26.5‰ Data points with different or the same letters at corresponding time intervals are significantly or not significantly different, respectively (analysis of variance, LSD = 0.98 at 0.05 confidence level).

TABLE 2.

Percent Clams Siphoning at Various Salinities (Temperature 25°C)

Salinity (‰)	% Siphoning	(# clams)
15	0	(28)
20	4.2	(47)
25	83.3	(48)
30	89.6	(48)

The percentage of clams observed siphoning at different salinities and temperatures was recorded. At a temperature of 25°C, salinities of 25‰ and 30‰ showed the highest percentage of siphoning clams (Table 2). Few siphoning clams were observed at 20‰ At a salinity of 26.5‰, temperatures of 20° and 25°C showed the highest percent siphoning clams (Table 3). A low percentage of siphoning clams was observed at 30°C and none were seen at 16°C.

DISCUSSION

Bacterial loads in clams showed seasonal variation with relatively low counts in colder months and higher counts in warmer months. Clams accumulated up to 1.5 × 10^7 cfu/gram shucked clam (September, 1985). Accumulation occurred even though water from the Colleton River Estuary contained low fecal coliform counts and undetectable levels of *Salmonella* and *Shigella* spp. in clams and would be considered unpolluted from sewage. Shellfish accumulate microorganisms through filter feeding, especially during warmer seasons when temperatures promote siphoning (Van Winkle *et al.* 1976) and bacterial counts are highest in natural waters (Zobell 1946). *Vibrio parahaemolyticus*, an indigenous bacterium in estuaries, was accumulated only in low numbers in clams, indicating low population levels in this area. Nevertheless, its presence indicates a potential public health problem if appropriate handling and processing of clams are not stringently followed. A number of food-borne illnesses have resulted from improper handling or cooking of seafoods contaminated with *Vibrio parahaemolyticus* (Center for Disease Control 1981, Idler 1970, and Wood 1970).

Using clams that were preloaded with an indicator bacterium (chloramphenicol-resistant *E. coli*), at concentrations comparable to *in situ* levels, allowed for observation of depuration. Temperature and salinity are two important parameters that affect depuration. Effects of temperature

TABLE 3.

Percent Clams Siphoning at Various Temperatures (Salinity 26.5 ‰)

Temperature (°C)	% Siphoning	(# clams)
16	0	(97)
20	83.7	(257)
25	78.2	(284)
30	33.5	(227)

and salinity on depuration are known to vary with the kind of shellfish, bacterial load and turbidity of the water (Cantelmo and Carter 1984, Eyles and Davey 1984, Hartland and Timoney 1979, Heffernan and Cabelli 1970, Janssen 1974, Ledo *et al.* 1983, MacMillan and Redman 1971, Perkins *et al.* 1980, Ritchie 1976, Rowse and Fleet 1984, Timoney and Abston, 1984 and Van Winkle *et al.* 1976). Other studies have indicated that a temperature range of 25°C to as low as 10°C (Hartland and Timoney 1979, MacMillan and Redman 1971, Perkins *et al.* 1980, and Van Winkle *et al.* 1976) and a salinity range of 24‰ to as low as 20‰ (Hartland and Timoney 1979, Heffernan and Cabelli 1970, MacMillan and Redman 1971, Timoney and Abston 1984, and Van Winkle *et al.* 1976) would give good depuration results for hard clams in New York (Cantelmo and Carter 1984 and MacMillan and Redman 1971) and England (Houser 1964). Our results show that a higher temperature (24–28°C) and salinity (24–31‰) range would be necessary for optimal hard clam depuration in South Carolina. These variations in environmental requirements for depuration may reflect adaptation of hard clams to regional differences in water temperature and salinity.

In order to depurate microorganisms from clams, it is likely that the water temperature will need to be changed form the *in situ* temperatures of clam beds. In the summer, the temperature of South Carolina coastal waters may exceed 30°C. Higher temperatures do not promote the shelf-life of fresh clams during processing and marketing (Furfari 1966). Therefore, it would be beneficial if depuration temperatures were lowered. Similarly, in the winter, when temperatures are low (approximately 16°C), decreased siphoning by clams is expected. Although bacterial loads in clams will also be reduced due to decreased siphoning, a low temperature will inhibit further depuration. Temperatures will need to be shifted upward for significant depuration to occur. Heffernan and Cabelli (1970) showed a marked decrease in siphoning when clams were removed from 10°C and placed in 20°C water. However, our results indicated that clams acclimated to 20°C could be shifted to a higher optimal temperature for better depuration without apparent "thermal shock." The difference in the range of temperatures used in these experiments may account for the difference in results. In contrast, our findings show that clams acclimated at a higher temperature and shifted to a lower temperature had a lower rate of depuration compared to clams that were both acclimated and depurated at the same lower temperature. Longer depuration times would be required to overcome this "cold shock" on depuration.

In our depuration studies, clams were preloaded with indicator bacteria prior to monitoring depuration. However, only clams that had siphons visibly extended at the end of the loading period were used in depuration experiments. It is not known whether clams siphon intermittently or throughout a loading or depuration period. Nevertheless, at different salinities and temperatures there was a change in the number of clams that were observed siphoning. Our results showed that for siphoning clams, depuration would be best at approximately 24–31‰ salinity and at temperatures of approximately 24–28°C. However, the highest percentage of clams that were observed siphoning occurred at similar salinities but lower temperatures (20–25°C). Small numbers of "unsiphoning" clams would prolong required depuration times since they pose potential public health problems if consumed.

This study has shown that for *M. mercenaria* cultured in South Carolina coastal waters, a temperature and salinity close to 24°C and 24–31‰, respectively, would favor a high percentage of depurating clams and faster depuration. "Temperature shock" would also be more apparent when shifting from a high temperature to a lower temperature for depuration. Lowering the temperature should help promote the shelf-life of clams and maintain lower bacterial concentrations, but would also extend the period of the time required for effective depuration.

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A THEORETICAL EVALUATION OF SHELLFISH RESOURCE MANAGEMENT[1]

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ABSTRACT Resource management alternatives for three commercially important bivalve species (*Mya arenaria* Linne, *Mercenaria mercenaria* Linne and *Crassostrea virginica* Gmelin) are examined by applying population projection models and sensitivity analyses to age(stage)-specific life history information. All species showed positive correlations between size and fecundity and size and survivorship. Population growth rates were 2–3 orders of magnitude more sensitive to changes in survivorship in larval and juvenile stages of the life cycles than proportional changes in either survivorship or fecundity in adult size classes. The greatest return will be realized in shellfish production if management efforts are directed to increasing juvenile survivorship and the quality and/or quantity of the juvenile habitat.

KEY WORDS: Bivalve resource management, theoretical analysis

INTRODUCTION

Presently there exists a variety of shellfish resource management practices ranging from harvesting strategies which limit minimum size and quantity of adults that may be taken, to re-seeding programs which supplement local populations with artificially planted juveniles. Other policies include predator control, enhancing the suitability of potential larval settlement areas, and planting adults for spawning purposes. Conceptually, these resource management alternatives are dramatically different since each concentrates on a different portion of the organism's life history. To date, no quantitative attempt has been made to assess the relative benefits of the various programs. While their relative success can be assessed after implementation, realistically, it may be years before this is possible. An interim approach is to theoretically evaluate the various management policies using mathematical models.

It is obvious that the success of any management program is dependent upon the biology of the exploited species. For example, Adams (1980) illustrated the theoretical relationship between the harvestability and life history strategies of various fish species. He found that those species with more "r-selected" traits (e.g., fast growth, early maturity, production of large number of offspring) could withstand more intense harvesting than more "K-selected" (e.g., slow growth, delayed maturity) species. Only after understanding how a natural population maintains itself through time, is it possible to predict its response to human intervention.

To simplify the problem of comprehending how a population projects itself through time, it is often convenient to use demographic data as the parameters in mathematical models that depict the growth (or decline) of a population. One advantage of this type of analysis is that it computes a population growth rate which may then be used as a currency to assess the relative fitness of different suites of demographic parameters. After establishing baseline demographic data (e.g., life table), it is then possible to represent management policies demographically by identifying their impacts on the baseline data. Population growth rate resulting from the altered life table can then be used as a relative measure of the long-term impacts of various management alternatives on target species.

Matrix population models are commonly used for this purpose. These models have been used extensively for analyzing life history tactics (e.g., Hartshorn 1975; Longstaff 1977; Caswell and Werner 1978; Enright and Ogden 1979; Pinero et al. 1984; Levin et al. 1987) and optimum harvesting problems (e.g., Usher 1966; Beddington and Taylor 1973; Doubleday 1975; Rorres 1976; Gopalsamy 1976; Harley and Manson 1981). Since this is an age- or stage-classified model, it is possible to investigate processes which impact the population at specific isolated portions of the life history. For instance, Lefkovitch (1967) classified a population of insects by life stages and simulated differential stage-specific mortality rates, and Jensen (1971) used the Leslie matrix to determine the effect of increased juvenile mortality on trout population yield.

Bivalve management policies can be translated into changes in the demography of local populations. For example, planting spawner stocks may increase the fecundity of the population, re-seeding programs may increase survivorship of juveniles, and harvest strategies affect the survivorship of adults and fecundity of the population. In the present study, the Leslie matrix is used to analyze the life history tactics of three species of commercially important bivalves: *Mya arenaria* (Linne) (soft shell clam); *Mercenaria mercenaria* (Linne) (hard shell clam); and *Crassostrea virginica* (Gmelin) (American oyster). The relative benefits of commonly used resource management policies

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are then assessed in light of their differential impacts on various stages of the species' life cycles.

METHODS

The Leslie Matrix

The Leslie matrix is a linear, discrete, time invariant model, based on an age-structured population, that may be used to describe direction and magnitude of population growth, as well as the stable age distribution and reproductive value of each age class. A detailed description of the model appears in Pielou (1977). The dominant eigenvalue, λ_m is equal to e^r where r is the intrinsic rate of increase (Lotka 1925) and is used as a relative measure of evolutionary fitness (Fisher 1930).

An analysis of the relative importance of each of the parameters in the matrix, with respect to population growth rate, can be accomplished by sequentially changing single parameters in the matrix and observing the relative effect on λ_m. An alternative and more straightforward procedure, known as the sensitivity analysis, has been derived by Caswell (1978) and uses stable age distributions and reproductive values (right and left eigenvectors of the matrix, respectively) to assess the sensitivity of λ_m to proportional changes in fecundity and survivorship.

The Use of Leslie Matrices for Resource Management Problems

While the Leslie matrix has been frequently used for the analysis of life history strategies and optimum harvest problems, Mendelssohn (1976) has criticized the approach because it neglects density effects. Indeed, density dependence is intimately linked to the harvesting problem since if population growth is limited by intraspecific interactions then harvesting can change the demography of the harvested species. Sustained harvesting is most easily tolerated by those species that experience increased productivity after individuals have been removed. Simulated exploitation studies in the laboratory have documented enhanced productivity following removal of individuals (Nicholson 1954; Watt 1955; Slobodkin and Richman 1956; Sillman and Gutsell 1958; and Usher et al. 1971). Enhanced productivity may frequently be the result of diminished rates of mortality following decreases in population density (DeAngelis et al. 1977). Changes in population productivity result in changes in the matrix parameter values thereby violating the time invariant assumption of the model. Beddington (1974) mentioned that unless a population were in the middle of a colonizing episode or at a density below limiting resource levels, parameters of the matrix would be valid for only a few generations.

Analytical solutions to the density dependence problem have been incorporated into the matrix model (e.g., Leslie 1948; Pennycuick et al. 1968; Usher 1972; Van Winkle et al. 1978); however there is conflicting evidence that intraspecific interactions limit the population density of large bivalves. For example, while Peterson (1982) concluded that growth, fecundity, and recruitment of *Protothaca stamina* were all significantly reduced by increases in adult population density, Malinowski and Whitlatch (1988) found that adult growth, fecundity, survivorship and recruitment were not significantly affected by population density in *M. mercenaria*. In general, studies that have documented density-mediated growth effects in *M. mercenaria* (e.g., Eldridge et al. 1979; Walker 1984; Hadley and Manzi 1984) have tested densities characteristic of aquacultural operations which may be an order of magnitude or higher than population densities normally encountered in natural populations. In addition, several studies have concluded that predation (particularly among the juvenile age classes) ultimately determines the distribution and abundance of *M. mercenaria* and *M. arenaria* (MacKenzie 1977; Blundon and Kennedy 1982; Malinowski and Whitlatch 1988). Therefore, the omission of density dependence from the model may not necessarily sacrifice realism and many objections to the use of the model may not be relevant. Other biological processes unique to organisms with a planktonic life stage do, however, violate the assumptions of the model. For example, populations of large bivalves experience intense annual variability with respect to successful recruitment (e.g., Carriker 1961; Saila et al. 1967) and since these bivalves have a one-to-three week larval stage, it is unlikely that larvae settling into a population originated solely from that population. Furthermore, the matrix parameters may be extremely site-specific and vary over relatively small spatial scales (Flagg and Malouf 1983; and Malinowski and Whitlatch 1988).

Solutions to the optimal yield problem require a precise prediction of the actual number and/or biomass of organisms in a population through time. Since these bivalve populations violate the assumptions of the model, it is clear that the model cannot be used to accurately predict the size of these populations through time. It is, however, possible to use this model to address a more general problem. Our purpose is to use the Leslie matrix in its simplest form in order to translate induced demographic changes into a meaningful population parameter such as population growth rate which can then be used as a measure to assess the relative importance of processes which affect the organism at specific stages of the life cycle.

Available Data and Analytical Procedures

To use the Leslie matrix model, only age- or stage-specific fecundity and survivorship data are needed. Life table data for each species were derived from the literature (Table 1). While there may be considerable variation in size among individuals of the same age class (e.g., Peterson et al. 1983) and both fecundity and survivorship are more closely correlated to size than age in these bivalves, age classes have been assigned to size class intervals for convenience in interspecific comparisons and presentation

TABLE 1.

Survivorship (l_x) and fecundity (m_x) data used in Leslie matrices for the three bivalve species.

Age	*C. virginica*[1]	*M. mercenaria*[2]	*M. arenaria*[3]
	SURVIVORSHIP		
Post-set	0.091	0.169	0.007
1	0.453	0.169	0.833
2	0.350	0.910	0.790
3	0.342	0.910	0.902
4	0.032	0.910	0.899
5		0.910	0.941
6		0.910	0.969
7		0.910	0.824
8		0.910	
	FECUNDITY (LOG)		
Age	*C. virginica*[4]	*M. mercenaria*[5]	*M. arenaria*[6]
Post-set			
1	6.24		
2	6.94		4.38
3	7.51	6.76	4.79
4	7.72	6.96	4.88
5	7.89	7.16	4.98
6		7.25	5.08
7		7.33	5.18
8		7.44	5.26

[1] Dame (1976) for 0–1 year old; Mackin (1961) for 1+ age-classes.
[2] Connell et al. (1981) for juveniles; Carriker (1961) for adults.
[3] Modified from Brousseau (1978a) where $l_x = 1 - q_x$ and then collapsing the life table so it represents yearly age intervals.
[4] Estimated from Davis and Chanley (1956) for a 40 ml (interval shell volume) individual and then extrapolating for other ages using regression equation of Dame (1976, p. 248).
[5] Estimated from Davis and Chanley (1956) for a 65 ml (internal shell volume) individual and then extrapolating for other ages using regression equation of Hibbert (1977).
[6] Modified from Brousseau (1977b).

of results. Of the three species in question, a single study summary of a complete life table is only available for *M. arenaria* (Brousseau 1978a). Larval survivorship has not been documented for any of the bivalves. Vaughn and Saila (1976) derived a formula for indirectly computing survivorship of an age-class if all other life table parameters are known. This equation was used to determine the minimum larval survivorship necessary to generate a stable population. The compiled life tables should be viewed only as generalized descriptions of the demography of each species. These species share the characteristics of high fecundity which increases with size/age, low larval and juvenile survivorship and high adult survivorship. These characteristics, rather than the exact life table values, are under scrutiny in the present analyses.

For each species the Leslie matrix model was run with larval settlement rates varying from 100% to 1×10^{-8}%. The model was also used to evaluate the effect on population growth rate of three harvesting strategies, each removing the same number of individuals but concentrated harvesting on different age classes within the populations. Sensitivity analyses, as derived by Caswell (1978), were used to determine the relative effects of altering age-specific fecundity and survivorship on the population growth rate.

RESULTS AND DISCUSSION

The life history tactics (*sensu* Stearns 1976) of each of these bivalves examined are characterized by high fecundity, iteroparity, large size, and high larval and juvenile mortality (relative to adults). Consequently, the analyses of the different species yielded approximately similar results and the species will be discussed collectively.

While it was possible to estimate most parameters of the life tables, larval and early post set mortality was deduced indirectly from the other parameters of the life table. Assuming 100% survivorship during this stage of the life history resulted in population growth rates (λ_m ranging from 20.69 for *C. virginica* to 3.30 for *M. arenaria*. Larval survivorship values that yielded a stable population (e.g., $\lambda_m = 1$) range from about 0.1% to 0.0001% (Table 2). These values were used for all subsequent analyses except simulated harvests (see Figures 3–4).

Current commercial shellfish management policies have taken many forms and while the ultimate goal of each is to increase yield of the fishery, there have been no attempts to quantitatively determine the relative effectiveness of each policy. The establishment of minimum harvest sizes serves at least two purposes. First, by allowing the harvest of only large individuals, potential yield (biomass) of a single cohort is increased (provided adult survivorship is high). A second purpose, and one more relevent to the present analysis, is that larger individuals realize increased fecundity and the reproductive contribution of a cohort to future generations will be increased as the minimum harvestable size increases. For example, Bricelj and Malouf (1981) and McHugh (1981) suggest that current hard shell minimum size limits and harvest strategies which concentrate on small individuals may not effectively protect adequate breeding stocks.

MacArthur (1960) reasoned that harvesting should be restricted to those older age classes with low reproductive values because the reproductive values of most organisms

TABLE 2.

Population growth rates (λ_m) assuming 100% larval survivorship and the larval survivorship that will yield a stable ($\lambda_m = 1$) population (critical larval survivorship) for each species.

Species	λ_m	Critical Larval Survivorship[1]
M. mercenaria	9.59	1.1×10^{-6}
M. arenaria	3.30	6.7×10^{-4}
C. virginica	20.69	8.0×10^{-7}

[1] Computed from equation given by Vaughn and Saila (1976).

peak early in life and then decline throughout adulthood. The three bivalves examined here deviate from this general pattern. The reproductive values peak early in life and, since fecundity is size related, remain high throughout adulthood (Figure 1). Coupled with stable age distributions, reproductive values are used to compute the survivorship sensitivity analyses (Caswell 1978) which apply directly to the determination of optimal harvest sizes. Sensitivity of λ_m to changes in survival describes the effect on population growth rate of proportional changes in age-specific survival or age-specific harvesting. In theory, harvesting should be concentrated on those age classes that contribute least to λ_m. Identification of a major change in slope of the survivorship sensitivity function (Figure 2) would suggest a logical minimum harvest size. Results, however, indicate that there are only slight differences in the sensitivity of λ_m to changes in survivorship among the adult (>2 years old) age classes. Therefore, removing a certain proportion of an old age class is essentially equivalent to removing that same proportion of three or four year olds. Any age class may be harvested with approximately equivalent effects on the population growth rate provided minimum size limits allow the organism to reach reproductive maturity and spawn.

Since predation is generally the cause for extremely high rates of juvenile mortality (MacKenzie 1977; Blundon and Kennedy 1982; Malinowski and Whitlatch 1988), both reseeding beds and predator control are synonymous with increasing juvenile survival. The sensitivity of λ_m to changes in survivorship (Figure 2) indicates that population growth rate is most affected by alterations in juvenile survivorship. In fact, there are at least two orders of magnitude difference between adult and juvenile survivorship. Reductions in juvenile mortality will have 100 times the impact on the future number of individuals in the population than a proportional reduction in adult mortality, suggesting that protecting the juvenile stages of the life history rather than establishing size-specific harvest strategies would be a more beneficial management policy for the three species examined. To assess the relative benefits of these two alternatives, three different harvest strategies were simulated on *M. arenaria* and compared with reductions in juvenile survivorship. Each harvest strategy removed 97% of the adult population and differed with respect to the intensity of the age-specific removal. Despite drastic differences between harvest strategies, there was little difference with respect to effects on the population growth rate (Figure 3) and, when compared to simulated reductions in juvenile survivorship (Figure 4), indicate that removing 97% of the adults is equivalent to decreasing juvenile survivorship from 0.7 to 0.3%.

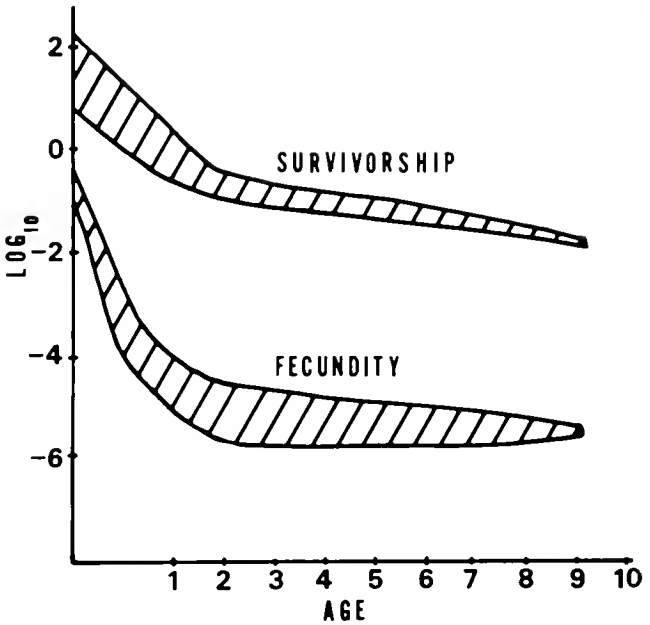

Figure 2. The relative sensitivity of the population growth rate (λ_m) to single matrix parameter changes in survivorship and fecundity [equations derived by Caswell (1978)]. The shaded area encompasses all values of all three species of bivalves.

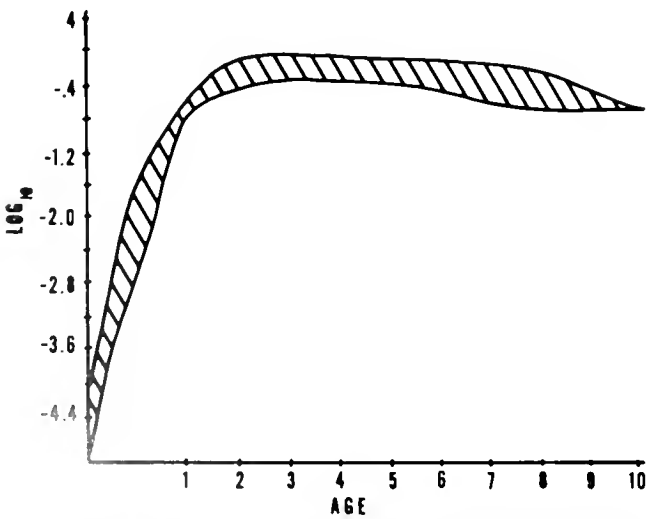

Figure 1. Age-specific reproductive values given by the left eigenvector of the Leslie matrix. The shaded area encompasses all values of all three species.

Sensitivity analyses can also be used to evaluate the relative effectiveness of planting adult shellfish for spawning purposes as compared to the alternative strategy of increasing the survivorship of juveniles. The consequences of increasing reproductive potential of the population can be examined by determining the magnitude of the response of λ_m. A comparison of the sensitivity of λ_m to changes in fecundity with respect to changes in survivorship reveals a dramatic result. In all cases, population growth rate is at least four orders of magnitude more sensitive to changes in juvenile survivorship than it is to deviations in fecundity of adults (Figure 2). Since larval and early post set settlement mortality rates are extremely high, very large increases in fecundity are necessary to duplicate the consequence of

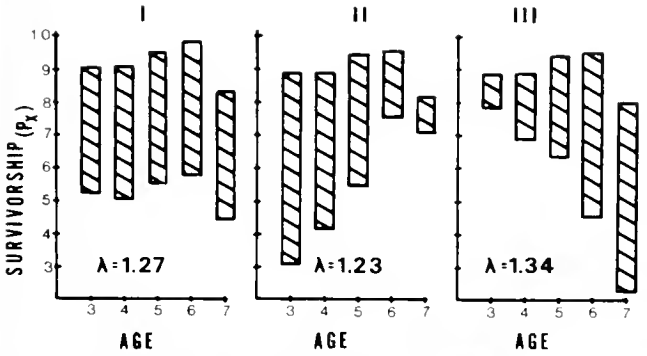

Figure 3. Simulated harvesting strategies of *M. arenaria*. Each strategy removed 97% of the adults in the population but concentrated on different adult age classes (Strategy I: equal intensity of harvesting on all adult age classes; Strategy II: concentrated harvesting on older adult age classes). The shaded areas represent the age-specific decreases in survivorship resulting from the simulated harvesting. The relative effect of each strategy on the population is assessed by comparing the resultant values of λ_m = (λ_m 1.43 before harvesting). A larval survivorship of 0.01 was arbitrarily chosen for these simulations.

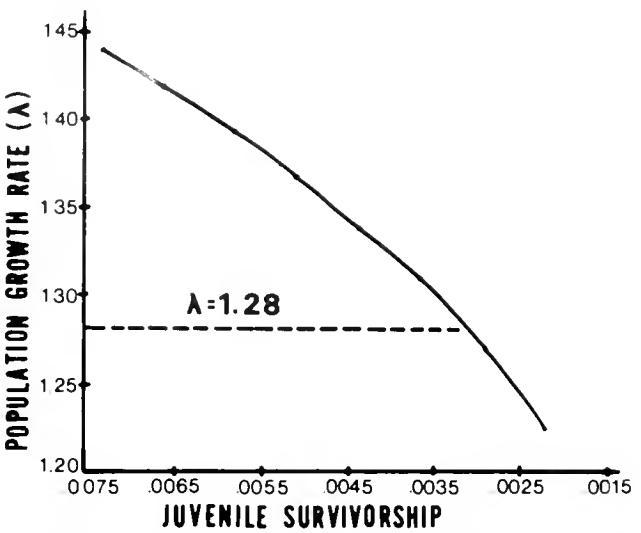

Figure 4. The effect of simulated reductions in juvenile survivorship on the population growth rate (λ_m) of *M. arenaria*. A larval survivorship value of 0.01 was arbitrarily chosen for these simulations (Figure 3). λ_m = 1.28 corresponds to the average value of m resulting from the harvest simulations shown in Figure 3.

only slight increases in juvenile survivorship. Furthermore, Kasner and Malouf (1982) have demonstrated that a basic assumption of the spawner transplant concept is incorrect (transplanted clams spawned at the same time as native clams) and estimate that recruitment resulting from typical spawner transplants will be insignificant compared to contributions from native standing stocks.

These results suggest that far greater return may be gained from management efforts aimed at increasing juvenile survivorship than from other alternatives. In a comparison of several natural populations of *M. mercenaria*, MacKenzie (1977) arrived at a similar conclusion. He found differences in densities of adult clams between local populations were correlated to the abundance of juvenile clam predators and observed a 7–8 fold increase in clam density after juvenile clam predators were poisoned. MacKenzie (1979) further suggested practical techniques of increasing clam abundance which focused on the juvenile stage of the life history. Since juvenile bivalves (1–10 mm shell length) may experience intense predator-mediated density dependent mortality (Boulding and Hay 1984; Malinowski and Whitlatch 1988), it is possible that increased recruitment (resulting from spawner transplants or increased average size of adults) will be followed by increased rates of predation. By similar reasoning, the return on seed plantings is not likely to be greater than the harvest of the individuals planted (there will be little if any contribution to future generations). It appears, therefore, that persistent juvenile clam predator control has the greatest potential to significantly increase the maximum sustainable harvest of these species.

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ABSTRACTS OF TECHNICAL PAPERS

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PATHWAYS OF SILVER ACCUMULATION BY THE AMERICAN OYSTER (*CRASSOSTREA VIRGINICA* GMELIN) IN CHESAPEAKE BAY

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Because of low-level aquatic releases of radioactive ^{110m}Ag (silver) from some nuclear power plants, and because of the limited information on the effects of these releases, a series of studies was conducted to investigate processes and pathways of Ag accumulation by oysters (*Crassostrea virginica*). During 1984 and 1985 three pathways were examined at three temperatures. Groups of 50- to 70-mm hatchery-reared oysters (0.97 to 1.13 g initial dry weight) were exposed to stable Ag from several sources including enriched water (5 $\mu g \cdot l^{-1}$), enriched sediment (1.76 $\mu g \cdot g^{-1}$), enriched algae (77.6 $\mu g \cdot g^{-1}$), and a combination of these three at 15°, 20° and 25°. Ag was rapidly accumulated in soft tissues over a 3- to 4-week period until body burdens were nearly five times controls (4.02 vs. 0.83 μg Ag $\cdot$ oyster^{-1}), except for oysters exposed to enriched sediment which probably rejected the sediment as pseudofeces. Ag body burdens rapidly decreased during subsequent depuration periods, but after 9 weeks the oysters from the enriched water, algae and combination tanks still averaged 1.7 times the Ag found in controls (1.46 vs. 0.85 μg Ag $\cdot$ oyster^{-1}).

It is clear that oysters accumulate Ag from water, but not from sediment. The degree to which Ag is accumulated from algae, however, is still in question as experiments yielded conflicting results. Uptake rates increased with temperature, but differences among rates at 15°, 20° and 25° were small. These studies indicate that the primary source of Ag accumulated by oysters is dissolved in water and not in particulate form.

CYTOLOGY OF GAMETOGENESIS IN TRIPLOID PACIFIC OYSTER, *CRASSOSTREA GIGAS*

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Diploid and triploid cohorts were reared together in Eureka, CA and sampled histologically at two to four week intervals during their first reproductive season. Flow cytometry of somatic tissue confirmed ploidy; this same analysis on gonadal tissue provided information on distribution of DNA content in component cell types. Relative maturity was compared by quantifying cross sectional area of gonad relative to total area.

Diploid oysters matured normally, relative maturity was equal between sexes, and all spawned at the end of July. Glycogen content decreased by 72% prior to spawning and increased afterward.

Triploids matured abnormally. Females matured less than males, producing few oocytes and mobilizing less glycogen during maturation. Males matured about half as much as diploids but twice as much as triploid females. Glycogen levels in triploids decreased only 8% prior to spawning but continued to decline for eight more weeks.

Greater maturity in males resulted from mitotic proliferation during maturation. Cytofluorometric results indicate that some meiosis does occur in triploid males, resulting in aneuploid gametes. Cell cycle analysis on dividing tissues suggests the rate, in addition to extent, of gametogenesis is retarded.

Twenty percent of triploids but no diploids were hermaphroditic. Excluding hermaphrodites, sex ratios in diploids and triploids were the same, although males were significantly more frequent in earlier sampling periods, i.e. sexes were heterogeneously dispersed within the gametogenic period. Surprisingly triploids also spawned.

Aspects of reproductive biology in diploids, inferred from aberrant maturity in triploids, are discussed.

AGE AND MEAT YIELD OF STIMPSON'S SURF CLAM, *SPISULA POLYNYMA*, A RECENTLY FOUND COMMERCIAL BIVALVE RESOURCE IN EASTERN CANADA

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Exploratory surveys conducted between 1980 and 1983 by the Invertebrates and Marine Plants Division, Department of Fisheries and Oceans, Halifax, described commercially harvestable concentrations of Stimpson's surf clam, *Spisula polynyma*, on the Scotian Shelf. Preliminary estimates of virgin biomass on Banquereau Bank were upward of 750,000 t. This species is thought to have commercial potential similar to the economically important Atlantic surf clam, *Spisula solidissima*, being harvested in the eastern United States. A commercial test fishery is in progress, and this study is intended to provide biological information pertaining to age and meat yield of *S. polynyma* essential for resource management.

Random samples representative of the size range were collected during the 1980–83 research surveys and the test fishery. Gear selectivity resulted in the minimum observed shell length at 24 mm, while the largest was 157 mm. A total of 355 shells ranging from 24 mm to 143 mm were aged by taking thin sections (approximately 0.25 mm thick) across the chondrophores and counting age lines using a light microscope, as described by Ropes (1984). Length/age relationships were determined for selected areas of Banquereau Bank and were compared with *S. polynyma* in Alaskan waters (Hughes and Brown 1981). More than 4,000 fresh-frozen clams from the research surveys were analysed to determine meat yield and were cross checked with fresh clams obtained from the test fishery. Meat yields ranging from 35.5% to 44.7% were compared with the clams in Alaskan waters and with *S. solidissima* being harvested in the U.S. fishery.

ASSESSMENT OF MORTALITY IN AN OFFSHORE POPULATION OF QUEEN CONCH, AND COMPARATIVE NATURAL MORTALITY ESTIMATION IN MOLLUSKS

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A 2-year Jolly-Seber multiple tag-recapture experiment was conducted on a queen conch, *Strombus gigas* L., population offshore of La Parguera, PR in order to estimate mortality. Over 2000 individuals were tagged in 9 sampling periods spaced at 3-month intervals from August 1983 to August 1985. The occurrence of fishing during half the intervals allowed estimates to be made of both fishing and natural mortality. Fishing mortality averaged $F = 1.14$ over the study period. An upper limit of natural mortality $M = 1.53$, including effects of emigration, was estimated. Assuming random diffusion, emigration was estimated and subtracted yielding $M = 1.05$.

This and other reported estimates of M for queen conch are considerably higher than those reported for temperate mollusks. A preliminary relationship predicting M from von Bertalanffy growth parameters $P = \text{Log } k \cdot W\infty$ was developed. The regression of Log M vs P accounted for over 90% of the variability of M, making it useful for corroborating and comparing independently derived estimates. For queen conch, M was consistent with the relationship; other large tropical mollusks should also be expected to have high natural mortality rates.

INTERANNUAL VARIABILITY IN RECRUITMENT OF JUVENILLE DUNGENESS CRAB: IS AN ESTUARY IMPORTANT AFTER ALL?

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A working hypothesis during an ongoing study of juvenile *Cancer magister* population dynamics has been that major estuaries of the southern Washington coast (Grays Harbor and Willapa Bay) provide critical nursery habitat to a significant proportion of newly settled 0+ crab in comparison to those that settle directly nearshore. The estuarine population estimate of 0+, based only on subtidal surveys, supported this hypothesis in one year (1983) of three (1983–85). Otherwise, 0+ estimates for a nearshore coastal area (albeit much greater than the subtidal estuarine area) were as much as two orders of magnitude higher. Three provisos to this apparent refutation of our hypothesis are in order: 1) Estuarine 0+ grow much faster than nearshore siblings and are 2× larger and 7× heavier by September of the first year. This presumably imparts a survival advantage to the larger, estuarine siblings. 2) Intertidal population abundance of 0+ may be 2–3 orders of magnitude greater than subtidal estimates. Additional work to better quantify intertidal estuarine populations is needed to provide a better comparison between nearshore and estuarine 0+ abundance. 3) In all three years, 1+ population estimates for the estuaries have generally equalled or greatly exceeded estimates for the nearshore. Apparently the species occupies estuaries en masse for a second summer as 1+ juveniles. As the study proceeds, the general hypothesis has been retained that estuaries are of critical importance to *C. magister*, but our perspective as to location and habitat type used by 0+ and importance of the system to older juveniles has changed.

RESPONSE OF MEGAFAUNAL PREDATORS TO SYNCHRONOUS SETTLEMENT OF SESSILE PREY

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Direct underwater observations by biologist-divers have revealed small-scale aggregations of high density prey greatly influence nearfield predator populations. Synchronous and aggregative settlement of benthic prey (i.e., *Mytilus edulis, Modiolus modiolus, Balanus* spp., *Mercenaria mercenaria*) provide a short term prey pool which requires little or no search time once the patch is located by predators, thus facilitating prey capture.

Grasping/crushing predators (i.e., *Tautogolabrus adspersus*, *Cancer* spp., *Carcinus maenas*, *Pagurus* spp.) often forage on aggregative prey laterally along established fronts (the interface between a prey and non-prey area) which presents easier access to individual prey items. Non-grasping predators (i.e. Asteroidea) are not apparently selective to individual prey position within prey aggregations. These types of predators help establish fronts in high density prey patches for other species to cue on. Motile predators cue on other individuals which have located areas of easy prey access and also forage at these locations (social facilitation). Predators aggregate in prey patches, rapidly depleting prey densities to nearfield or lower densities. These predation events are highly localized (patchy), have short temporal scales, and have profound effects on the distribution and subsequent growth of prey species. In order to understand such events, high resolution (short-term) sampling is required.

REPRODUCTIVE SUCCESS IN TANNER (*CHIONOECETES BAIRDI*) AND DUNGENESS (*CANCER MAGISTER*) CRABS HELD ON OILED SEDIMENTS

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Gravid female Tanner (*Chionoecetes bairdi*) and Dungeness (*Cancer magister*) crabs were held on one of several concentrations (0–8.9 µl Cook Inlet crude oil/gm sediment) of oiled sediments through one complete reproductive cycle. These two species of commercially important crabs, although found in similar habitats but at different depths, exhibit somewhat different behavioral characteristics while carrying eggs. Brooding Dungeness crab females consistently bury in the sediments while gravid Tanner crab females rarely bury. Because of differences in behavior, we predicted dissimilar responses to oiled sediments.

Dungeness crabs held on all doses of oiled sediments produced significantly fewer numbers of larvae than did control crabs. Larvae from crabs in the high-dose tanks survived significantly shorter periods than did larvae from the control, low- and mid-dose tanks. Eggs from crabs in the high-dose tanks had significantly elevated levels of aromatic and aliphatic hydrocarbons, compared with eggs from control crabs.

Production of larvae and viability of larvae of Tanner crabs held on oiled sediments showed no differences from that of control crabs. Likewise, there was no significant uptake of hydrocarbons in eggs over levels found in controls.

We feel that the intimate contact of gravid Dungeness crabs with sediment-absorbed oil and oil present in interstitial waters in a polluted habitat can lead to reduced reproductive success in this species.

RELATIONSHIPS AMONG CONDITION INDEX, GLYCOGEN LEVEL, REPRODUCTIVE EFFORT, AND INTENSITY OF MSX (*HAPLOSPORIDIUM NELSONI*) INFECTION IN OYSTERS, *CRASSOSTREA VIRGINICA*

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As an initial attempt at describing the energetics of the MSX/oyster relationship, breeding stocks maintained in Delaware Bay, New Jersey were examined in May and June, 1985 for condition, glycogen level, and reproductive effort as well as intensity of infection by the haplosporidan parasite, MSX. Although slight differences occurred between the two months, oysters parasitized by MSX had less glycogen (% dry wt.), a lower condition index, and a reduced relative reproductive effort compared to non-infected oysters. These relationships were related to the intensity of infection, as oysters with systemic infections were affected to a greater extent than oysters with epithelial infections. The inter-relationship between condition, glycogen level, and gamete production was demonstrated by significant correlations between condition index and glycogen level, glycogen level and gonad index, and gonad index and condition index. It is presently unclear whether MSX is competing for glycogen reserves which in turn reduces reproductive effort or whether MSX interferes directly with normal gametogenesis, thus limiting the amount of glycogen being stored in the tissues.

GEOGRAPHICALLY WIDESPREAD BACTERIAL INFECTION AND MORTALITY IN PACIFIC OYSTERS, *CRASSOSTREA GIGAS*

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For the past ten years the University of Washington School of Fisheries has been studying mortalities of Pacific oysters in the Puget Sound basin. This study has focused on developing stocks of oysters through selective breeding which are resistant against summer mortality. Since 1981 oysters have been observed dying past the summer mortality period and on through December. These fall mortalities have been recorded in two bays in south Puget Sound. Similar occurrences have been reported from Willapa Bay and from several bays in British Columbia. Mortality is variable among the array of the selected experimental oyster stocks, ranging from 0 to 20%, suggesting a possibility of breeding for improved survival.

Over the last two years, the dying animals have been studied at the Center for Marine Disease Control at Battelle. Associated with the fall mortality pattern is the presence of a systemic bacterial infection of the oysters. In severely affected animals, green or yellow pustules occur on the mantle surface, on the gill, and in the adductor muscle and pericardial cavity. Histological examination of infected animals indicates the presence of a highly inflammatory, gram-variable, systematically distributed bacterium. Infections can be observed microscopically in clinically normal animals. The grossly visible pustules represent a terminal inflammatory response to the disease. Pathological observations and mortality data suggest that disease can be lethal in individuals and significant as a cause of mortalities in the populations of oysters.

Identity of the organism and the relationship of the disease to previously reported oyster diseases and mortalities will be discussed.

SUMMARY OF THE LOUISIANA OYSTER INDUSTRY DEPURATION CONFERENCE

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Louisiana's oyster industry produces about 12 million pounds of meat annually and provides more than 5,000 jobs. With 17 percent of the nation's classified shellfish waters, Louisiana has great potential for expanding production to offset declining employment in the mining sector. Yet all the state's shellfish waters are "conditionally approved" and subject to seasonal closures that have severely curtailed oyster production in recent years. Depuration affords a means to overcome environmental problems through technology, but its use for treatment of oysters from restricted waters to achieve public health standards is new to the state. Louisiana producers are experimenting with several approaches such as a batch-processing unit involving one-time use and disposal of seawater, a closed, recirculating system with biological filtration and ultraviolet light for bacterial reduction, and a flow-through system utilizing ozone for disinfection. Experience to date indicates that added costs of depuration can be offset by improved quality in terms of a cleaner shellstock product, the control of salty flavor, and longer shelf life, as well as the ability to meet mandated health standards.

The conference was held to provide current information about depuration to members of the oyster industry, regulatory agencies, financial institutions, governing bodies, academia, and the news media. A secondary purpose was to identify socioeconomic, regulatory, and technological factors that may inhibit the widespread practice of depuration in order to plan future research. The one-day conference dealt with the necessity for depuration and its effectiveness, state and federal regulations, economic aspects, the physiology of bacterial and viral accumulation and elimination, and the characteristics of depuration systems.

STATUS OF CONTROLLED PURIFICATION OF SHELLFISH IN THE SOUTHEASTERN UNITED STATES

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Increased competition for resources in the coastal zone along both the Southeastern Atlantic and Gulf Coasts has resulted in diminished quality and quantity of shellfish growing waters. In many coastal regions where water quality and shellfish resources are threatened by contamination from microbial pollutants, alternative technologies and processes have been implemented to promote responsible utilization of these resources. Controlled purification provides a practical method for cleansing potentially contaminated shellfish, insuring product quality, and protecting public health. Commercial purification operations and facilities vary between producing states and are contingent upon numerous controlling factors including species of shellfish, plant design specifications, water quality, microbiological criteria, and processing procedures. Each producing state is responsible for effectively regulating scheduled control purification processes (SCPP) according to recommended NSSP standards. The status of controlled purification processes, commercial operations, production levels, as well a a summary of guidelines regulating shellfish purification in the Southeastern States are presented.

PREDATION ON SINGLE SPAT OYSTERS *CRASSOSTREA VIRGINICA* (GMELIN) BY BLUE CRABS *CALLINECTES SAPIDUS* AND MUD CRABS *PANOPEUS HERBSTII* MILNE-EDWARDS

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Single spat oysters *Crassostrea virginica* of four size classes (3.4–24.6 mm mean shell heights (SH)) were exposed to six size classes of blue crabs *Callinectes sapidus* (9.3–85.5 mm mean carapace width (CW)) and five size classes of mud crabs *Panopeus herbstii* (7.1–34.4 mm mean CW) for two days. Crab predation, recorded as the number of dead oyster spat/crab/day, was directly proportional to crab size and inversely proportional to oyster size. Mud crabs of 34.4 mm CW and blue crabs of 85.5 mm CW had predation rates of 22.5 and 16.7 spat/crab/day on oyster spat of 24.6 and 24.4 mm SH, respectively. Larger sized spat could be more readily preyed upon by mud crabs than by blue crabs of similar size. Mud crabs of 7.1 and 25.2 mm CW caused significant mortalities to oyster spat of 8.1 and 24.6 mm SH, respectively. Blue crabs of 9.3, 24.5 and 85.5 mm CW caused significant mortalities to oyster spat of 3.4, 13.9 and 24.6 mm SH, respectively.

OYSTER BREEDING CAGES [OBC]—THE "ABOVE GROUND" GROWING SYSTEM

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The use of above ground cages to breed and farm oysters is a technique that has increased European oyster production by more than 30%. The concept—based on specially designed polyethylene cages—has dramatically improved the economics of oyster farming. The cage system increases the productivity of farming labor, enhances oyster growth and reduces the risks of oyster loss.

Three different style cages are used in the growing cycle. They are installed either on "breeding racks" or floated. Photos of typical European oyster farms are shown.

POSSIBLE INFLUENCE OF WIND ON *CANCER MAGISTER* SETTLEMENT

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Catch of *Cancer magister* along California, Oregon and Washington fluctuates cyclically. One proposed cause is an influence of oceanographic conditions on the larval stages. Analysis of available environmental data (upwelling index, surface temperature, sea level, and wind stress) showed a statistical relationship between catch and southward wind stress during the late larval period. The effect of wind on larvae depends on their vertical distribution. Preliminary sampling has indicated megalopae are neustonic at night and at low light levels, but distributed to at least 60 m in daylight. Implications of these results for a wind forced mechanism of larval recruitment are discussed.

SCALLOP BREEDING STUDIES

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Scallop breeding studies were undertaken to determine the feasibility of raising juveniles in a hatchery for aquaculture purposes. Three species of native scallops: weathervane, *Patinopecten caurinus;* rock, *Chlamys gigantea;* and spiny, *Chlamys hastata;* and two exotics, Japanese, *Patinopecten yessoensis;* and sea, *Placopecten magellanicus*, have been investigated. Most of the work has been with Japanese scallops and results for this species are described in detail. In 1985 about 25% of fertilized eggs of Japanese scallops developed to the veliger stage; 60 million veliger larvae were produced. Survival from veliger to metamorphosis stages was about 18.5%; 11.2 million mature larvae were produced. Larvae were fed single species or a mixture of five species of algae; *Isochrysis galbana*, Tahitian *Isochrysis; Chaetoceros calcitrans, Chaetoceros* sp. A.R.C. variety, and *Thalassiosira pseudonana*. Larvae developed from fertilized egg to metamorphosis in about 28 days when raised at 15°C. Several materials were used as cultch and five methods were used to settle metamorphosing larvae and raise spat; upwellers, downwellers, static water, flowing water in tanks and raceways. The best cultch was

"kinran" and the best method to raise spat was in flowing water or in raceways. About 50% of mature larvae metamorphosed but heavy unexplained mortalities were experienced in spat when about 0.4–0.6 mm shell height. About 1,500 juvenile Japanese scallops are being held in the natural environment to assess growth and mortality, the largest measure over 4 cm shell height.

Results of studies with other species are described briefly.

COMPARATIVE PHYSIOLOGY OF TWO COHORTS OF THE NORTHERN BAY SCALLOP, *ARGOPECTEN IRRADIANS IRRADIANS*

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Argopecten irradians undergoes rapid population decline in its second year of life. Mortality, growth and metabolic rates, and net growth efficiencies were compared for two cohorts of bay scallops held in cages between September 1984 and July 1985 at two sites in Long Island, N.Y. Mass natural mortality of second year scallops occurred in mid-winter (January through March), before the onset of a second reproductive period, and coincided with a period of minimal temperatures. At the site where milder environmental conditions prevailed, both cohorts maintained a positive energy balance throughout the fall, and experienced comparable tissue weight losses (9 and 11%) during the winter. The life span of Long Island bay scallops is thus estimated at 20 months. The main period of gametogenesis and gonadal buildup (April–May) did not coincide with the winter peak in phytoplankton abundance (Feb.–March).

Over the temperature range 1°C–23°C, metabolic rates of both year classes closely paralleled seasonal changes in water temperature. The latter explained a highly significant proportion (93%) of the seasonal variation in weight-specific oxygen consumption rate. An increase in oxygen uptake of first year olds was observed in conjunction with increased gametogenic activity in May. Metabolic rate during this period was about 50% higher than that predicted based on temperature alone, providing an estimate of the metabolic cost of reproduction in this species.

A HABITAT SUITABILITY INDEX MODEL FOR THE AQUACULTURE OF THE PACIFIC OYSTER, *CRASSOSTREA GIGAS*

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A Habitat Suitability Index (HSI) model was developed in order to evaluate the suitability of coastal areas in British Columbia for the aquaculture of *Crassostrea gigas*. In the model, the effects of abiotic and biotic factors upon oyster growth and mortality are quantified through the use of a relative index. Fundamental to the model is the comparison of existing habitat conditions to the optimum conditions of the habitat variables for the oyster as described in the literature.

The performance of the model was evaluated utilizing environmental and oyster production data collected from 10 field sites over a 14 month period. Site-specific HSI values derived from the environmental data were found to be significantly correlated with the increase in shell length of two groups of oysters which, over the course of the study, aged from 0–14 months ($r^2 = 0.82$, $p < 0.001$) and 14–28 months ($r^2 = 0.88$, $p < 0.001$).

The use of the HSI model in the selection of sites for aquaculture operations and in the management of coastal areas will be discussed.

BIOLOGY AND COMMERCIAL POTENTIAL OF GALATHEID CRABS IN BRITISH COLUMBIA

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The biology and commercial potential of the crab *Munida quadrispina* were examined by surveying the prawn fishermen and processors and by collecting data during prawn fishing expeditions in B.C. Photographic data from a previous study was analysed statistically to determine substrate preference. Pigment, lipid and protein contents were analysed to examine the potential for use of this species in fish food.

Fishermen believed that *M. quadrispina* is increasing in abundance as prawn stocks decline. A representative cruise and the surveys indicated that catches of 600 or more pounds of the crabs per day might be expected in some areas, in addition to similar catches of prawn.

Seasonal size frequency data indicate that growth rates of *M. quadrispina* are similar to other Pacific galatheid crab species. Females have a slower growth rate than males, and decline in abundance dramatically following reproduction in spring. Parasitism by isopods varied between sample locations. Substrate preference analyses indicated that *M. quadrispina* consistently prefer heterogeneous substrates (such as wood-fibre beds) to homogeneous ones, which may be related to hiding behaviour.

Proximate analysis indicated that carotenoid content is 2–3 times higher in *M. quadrispina* than in prawn or shrimp. Precent protein, lipid and pigment were higher in the waste portion than in the meat portion, suggesting a possible dual commercial use of tails for meat and waste portion for fish food.

PRELIMINARY RESULTS FROM THE STUDY OF ACQUIRED IMMUNITY IN THE OYSTER, *CRASSOSTREA VIRGINICA*

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For the determination of the concentration of antigen which will elicit a cellular response in oysters, preliminary experiments have been performed by challenging oysters with various concentrations of formalin-killed zoospores of *Perkinsus marinus*. Results indicate that a concentration of $0.07–2 \times 10^8$ formalin-killed zoospores could induce a cellular response (phagocytosis by hemocytes). The uptake of ^{14}C-labeled zoospores of *Perkinsus marinus*, *in vivo* and *in vitro*, by hemocytes from immunized oysters was shown to be higher than by hemocytes from control (non-immunized) oysters. Short-term exposure of oysters to the living pathogen also elicit a similar cellular response. Initial studies reveal that the composition of hemolymph in immunized oysters is different from that of control oysters.

LARVAL DEVELOPMENT OF THE SPINY SCALLOP, *CHLAMYS HASTATA* (SOWERBY)

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The early life history of the spiny scallop, *Chlamys hastata*, from gamete release through metamorphosis to a benthic juvenile, was observed and described. Ripe adults were induced to spawn by using a combination of UV-irradiated seawater and thermal stress. Newly released oocytes had a mean diameter of 71 μm and were surounded by a thick jelly coat. Larvae were planktotrophic and capable of metamorphosing about five weeks after fertilization when reared at 16°C (240 μm in valve length). Embryos and larvae at different developmental stages were prepared for scanning electron microscopy and histological examination to compliment live observations. Morphology of several key organs, valves, velum, gut, foot, and gill rudiment were examined. Structures described for the first time include the interlocking crown-and-groove feature on denticles of the larval hinge region, location of secretory cells on the outer margin of the velum, and specialized compound cilia at the mouth region.

Growth and survival of the larval stage was examined when reared at 12, 16, 19, and 24°C. Larvae reared at 12°C had a 42% survival, reached maximum valve length of 238.9 ± 0.93 μm and were capable of metamorphosis by 42 days, but were able to survive as larvae for as long as 130 days. Larvae reared at 16°C had a 33% survival, were able to metamorphose by 34 days and survived as larvae for as long as 115 days. Larvae reared at 19 and 24°C had slower growth and lower survival rates. Throughout development, valve length corresponded to valve height by a linear correlation ($r^2 = 0.87$) with a ratio of 1.1:1 for length to height.

THE POTENTIAL FOR DIRECT APPLICATION OF UNIVERSITY-DEVELOPED RESEARCH FINDINGS TO THE COMMERCIAL OYSTER INDUSTRY

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Recent research findings appear to have potential for direct application to the oyster culture industry. The most promising research involves the production of polyploid oysters using cytochalasin B; the use of chemicals to trigger metamorphosis and/or attachment of competent oyster lavae; and microencapsulation to potentially enable the formulation of complete diets to supplant microalgae, but to more realistically enable the easy addition of supplements and/or specific agents such as antibiotics and hormones. Other research with potential for application includes the development of techniques for gynogenesis to enable the acceleration of genetic selection of oysters and genetic engineering.

The direct application to commercial production-scale of findings developed at universities in small-scale laboratories is often not simple nor straight forward. Application to industry requires an intimate relationship between the university researchers who developed a concept and industry researchers who understand the requirements that must be met and limits to the application of the initial concept. In this presentation I shall use the above examples in attempting to explain the complexities and potential pitfalls in developing a working relationship between universities and private industry.

A SURVEY OF *PERKINSUS MARINUS* INFECTION IN THE GULF OF MEXICO

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Perkinsus marinus is an important cause of mortality in oyster populations in the Gulf of Mexico. Incidence of the disease has been related to salinity and temperature, however local variations in disease incidence among neighboring reefs are also well described. Infection by *Perkinsus* is being monitored in oysters in connection with NOAA's Status and Trends ("mussel watch") program. Fifty locations along the Gulf coast from southern Texas to southern Florida were sampled between January and April, 1986. To assess within site variability, twenty oysters were collected from each of three stations at each of the fifty sites. Mantle tissue from each oyster was cultured in thioglycollate medium. Preliminary results of *Perkinsus* incidence and intensity at each site are reported.

GROWTH RATE AND AGE STRUCTURE COMPARISONS OF GEOGRAPHICALLY ISOLATED HARD CLAM, *MERCENARIA MERCENARIA*, POPULATIONS

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Samples were collected from five geographically isolated hard clam populations in eastern Long Island Sound. Age determinations were made by counting the internal annuli of transversally sectioned valves. The von Bertalanffy growth model was used to generate growth parameters for each population. The parameter w (the growth rate at t_0) was used for statistical comparisons between populations.

A total of 896 clams were collected from the five sites and aged. Recruitment into each population occurred at generally low levels with strong year classes occurring aperiodically. Strong year classes were not found simultaneously at more than one site. This suggests that site specific factors, such as, differential predation or settlement or both, may be governing recruitment. Strong year classes were rare and as few as 4 year classes dominated a single population. Growth rates, using the w parameter, were significantly different between all populations. Differences in water depth, and therefore temperature and food availability, are proposed to explain growth differences. The implications of these results are discussed with regard to management schemes.

ENERGETICS OF STERILE TRIPLOID OYSTERS UNCOUPLE THE REPRODUCTIVE AND SOMATIC EFFORT OF DIPLOIDS

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Discrete energy budget analyses of diploid and triploid oysters, *Crassostrea gigas*, were made under ambient conditions of temperature, salinity and seston levels during the period corresponding to peak reproductive condition in diploids. Results indicate that ripe yearling diploid oysters are in negative energy balance while triploid siblings remain in a state of positive energy balance. Both reduced metabolic costs (measured as VO_2) and nitrogen excretion (VNH_3-N) in triploids specifically contribute to significant differences in the energy available for tissue production. Lower O/N ratios in diploids suggest that germinal tissue production coupled with relatively warm water temperatures may contribute to a stress condition and negative energy balance at this time of year. Rates of consumption and efficiency of absorption were similar for diploids and triploids.

Histological analyses of cross-sectional areas in diploid and triploid oysters demonstrate the virtual exclusion of gametes in female triploids and reduction in gametes in male triploids compared to the normal proliferation of gametes in sibling diploids.

Sterile triploids provide a means of assessing the significant impact that seasonal reproductive cycles have on the physiology of bivalve molluscs and may be estimated in terms of reduced metabolic costs and increased somatic growth in sterile triploids serving as synchronous controls. Recent models of reproductive effort in invertebrates are discussd with reference to metabolic costs associated with reproduction.

COMPARATIVE COASTAL ECOLOGY OF THE TROPICAL ROCKY-INTERTIDAL SNAIL *CITTARIUM PICA* IN THE EXUMA ISLANDS, BAHAMAS

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The population ecology of *Cittarium pica* was studied on shores of low, intermediate and high wave exposure, using both population sampling (114 sites) and transplant experiments (14 sites).

When compared to quiet sites, more exposed sites had higher population densities and highe densities of predators. At more exposed sites the snails showed higher rates of dispersal and mortality, and lower rates of growth. Dead shells from more exposed sites showed a higher proportion of lethal shell damage due to drilling predators. The decrease in mortality with increase in size was most pronounced at the more exposed sites. Size of maturation and relative fecundity were least at the more exposed sites. Coastal differences in population structure were consistent with coastal differences in growth and mortality, and were not ascribed to differences in recruitment pattern. The results suggest that low population densities at quiet sites are due to poor recruitment.

OPTIMAL INDUCTION OF TRIPLOIDY IN *CRASSOSTREA GIGAS* DEPENDS ON TEMPERATURE

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Egg lots from six mass spawns were treated using cytochalasin B (CB) from fertilization to past first cleavage at three different temperatures, 18, 20 and 25°C. Treatments of 1 mg CB/l were applied at 0, 15, 30, . . . , and 120 min after fertilization for the lowest temperature, 18°C. After 15 minutes the eggs were then filtered and resuspended in a 0.1% DMSO bath for another 15 minutes. Replicates were run for most treatments. Control eggs were exposed to 0.1% DMSO for 15 minutes at the appropriate temperature and time. Triploid percentages, larval growth and survival rates were measured to determine the optimal treatment at each temperature.

Large differences in survival to straight hinge were found among mass spawns. Some treated groups outperformed controls, but on average CB reduced larval survival during the first 48 hrs in all treated groups. This was most apparent during critical periods of zygotic development (e.g., fertilization). After 48 hrs, survival rates were not significantly different among control and treatment groups.

No significant differenees in growth were found between treated and control groups from the same spawn and having similar densities.

Replicates yielded similar percentages of triploids with standard errors below 10%. Induction curves were derived for each temperature. These curves illustrate that lower temperatures produced fewer triploids in their best treatments; highest percentages attained at 18, 20 and 25°C were 62, 74 and 88%, respectively. In addition, lowering the temperature delayed these maximum peaks; maxima at 18, 20 and 25°C are approximately 50, 45 and 30 min post-fertilization, respectively. Overall, the optimal treatment for inducing triploidy in the Pacific osyter (*C. gigas*) appears to be 30–45 min at 25°C whieh yielded 88 +/− 9% (SE) triploidy over four replicates.

THE IMPORTANCE OF INTERTIDAL SHELL AS NURSERY HABITAT FOR YOUNG-OF-THE-YEAR DUNGENESS CRAB IN GRAYS HARBOR, WASHINGTON

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Studies of juvenile Dungeness crab ecology and population dynamics in Grays Harbor (1983–85) show that intertidal areas, particularly those with an overlying shell substrate, play a critical role in the survival of newly recruited 0+ crab. Optimal habitat in Grays Harbor consists of shell depoits of the eastern softshell clam *Mya arenaria* and live commercial oyster beds (*Crassostrea gigas*).

Recruitment to the intertidal was monitored for 3 summers with an intensive study initiated in May 1985. Although initial settlement densities in May of 1983 were as high as 362 crabs/m^2, numbers fell to much lower but relatively stable levels of 15–20 crabs/m^2 in June and 5–10 crabs/m^2 in July and August of all 3 years. Even at these densities, population estimates were much higher for 0+ crabs in the intertidal subtidal areas where 1+ juveniles are prevalent.

Crabs greater than 40 mm carapace width were rarely found in the intertidal indicating that they 1) physically outgrow the shell habitat; 2) leave due to agonistic behavior and displacement and/or; 3) can no longer find suitable prey. This exodus from the intertidal to the subtidal in late summer may be the source of distinct increases in subtidal 0+ populations in September and October. Movement from shell refuge may also indicate attainment of size refuge since crabs of 30–40 mm CW at this time are not nearly so vulnerable to predation as are small, early summer instars.

DESTRUCTION OF BIVALVE MOLLUSC HINGE LIGAMENT BY CYTOPHAGA-LIKE BACTERIA: ASSOCIATION WITH MORTALITY IN HATCHERY-REARED JUVENILE PACIFIC OSYTERS, *CRASSOSTREA GIGAS*

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Histopathological examination of individuals from captive populations of juvenile Pacific oysters, *Crassostrea gigas*, experiencing high mortality levels revealed the presence of severe degenerative bacterial lesions in the hinge ligament. The ligament lesions were associated with bacterial infections in mantle and connective tissues. Ultrastructure of infeeted hinge ligament demonstrated a morphologicaly distinct and homogeneous bacterial population at the eroding ligament surface. Bacterial isolations from hinge ligaments of juvenile oysters in high-mortality populations yielded cytophaga-like bacteria as the dominant flora. These isolates are morphologically identical to bacteria associated ultrastructurally with ligament destruction. Among the bacterial taxa isolated from hinge ligament, the cytophaga-like isolates demonstrate a unique capability for *in vitro* proliferation using hinge ligament as the sole source of organic carbon and nitrogen. Colonization of oyster resilium by these isolates results in liquifaction or loss of mechanical resiliency. Serological and biochemical tests suggest that these bacterial isolates belong in the genus *Cytophaga* and are previously undescribed. Fitness consequences of hinge ligament loss are discussed in light of ligament structure and function.

DEPURATION OF HEAVY METALS BY HARD CLAMS, *MERCENARIA MERCENARIA*

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Hard clams, *Mercenaria mercenaria*, were exposed separately to three isotopes, ^{109}Cd, ^{51}Cr and ^{65}Zn for a period of 15 days after which the label was removed and depuration followed for one to several months. Depuration is a function of temperature and time but even at optimal temperatures (20°C) removal of metals by clams is slow compared to bacterial depuration. After 14 days of depurating $^{65}Zinc$, the digestive gland showed the highest percentage of removing the metal (56%) followed by the gills (36%), foot (31%) and mantle (27%); several organs however, increased their concentration of metal: the adductor muscle (102%), gonad (114%) and the kidney, as expected, concentrated the metal the greatest (157%).

If ^{109}Cd depuration is allowed to proceed for 45 days at optimal temperatures all organs show a decrease in metal content with the digestive gland having a 74% depuration followed by kidney (69%), mantle (51%), foot (40%), gill (31%) and adductor muscle (7%).

Depuration of ^{51}Cr at average temperatures of 15°C for 35 days showed the digestive gland again to have the greatest percent depuration (91%) followed by the mantle (77%), gill (76%), foot (72%), adductor muscle (65%) and kidney (49%).

In the process of depuration of heavy metals by clams several important factors are noteworthy: (1) depuration is a slow process even at optimal temperatures, the time period being months instead of days in the case of bacterial depuration, (2) different organs depurate at different rates depending on the metal involved, (3) clams shift the metal burden during depuration usually from the digestive gland and gills to the kidney for final elimination, (4) the adductor muscle consistently showed the lowest levels of activity of all organs studied both during uptake as well as throughout the depuration process.

BONAMIA OSTREA DISEASE OF THE EUROPEAN FLAT OYSTER (*OSTREA EDULIS*) IN NORTH AMERICA: OCCURRENCE, ENVIRONMENTAL EFFECTS AND HOST RANGE

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The European flat oyster, *Ostrea edulis*, is cultured in relatively small numbers in western North America. During 1985 and 1986, flat oysters from 12 locations in western North America were examined in the laboratory using a minimum 60-day elevated temperature regime, clinical, and histological methods. Oysters from three sites in Washington State, U.S.A., were discovered to be infected with a haplosporidian parasite of the amebocytes, identical in ultrastructure and disease manifestation to *Bonamia ostreae*, which is known to cause substantial oyster mortalities in Europe.

Laboratory studies showed that infected stocks of animals would manifest the terminal signs of the disease and die at 16°C but animals from the same stocks exhibited no clinicals signs of the disease or mortalities when held for up to six months at 8°C. In oysters which were sampled in June, prior to exposure to warming summer temperatures, the disease could not be detected by histological methods. However, individuals from the same groups exhibited the disease when held for 45 days at 15°C. During a 5-month period of exposure of *Crassostrea gigas* and *Ostrea lurida* to *Ostrea edulis* known to be infected with *Bonamia*, the disease was not detected in these two species. The localization of the parasite in amebocytes suggests that the animal's ability to dispose of invading infectious agents is severely impaired. Transmission of

the disease appears to be limited by environmental factors in the areas where it has been discovered.

TRANSPLANT OF ABALONE IN BARKLEY SOUND, BRITISH COLUMBIA

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Biological and economic feasibilities of transplanting sub-legal-sized abalone *(Haliotis kamtschatkana)* from exposed beds to more sheltered, productive abalone habitat were investigated. After nine months, recovery and growth of transplanted, tagged abalone were significantly better than nontransplanted, tagged controls. Recovery rates were 38% and 71% at the two replicate transplant sites. This difference was attributed to variation in both habitat composition and topography, which affected relative survey ease and success, and predator presence. There was little evidence of extensive emigration of transplanted abalone from the transplant sites.

The study demonstrates that it is biologically feasible to transplant abalone 50 to 100 mm in length. Economic feasibility is dependent on recovery rates attained, which is quite site specific. The population dynamics of abalone in exposed beds and the long-term potential for enhancing juvenile abalone settlement in abalone-depleted areas by transplanting adult broodstock into them are two remaining elements which need investigation to establish the overall biological merit of abalone transplants.

ENERGY STORAGE AND UTILIZATION IN THE BAY SCALLOP, *ARGOPECTEN IRRADIANS*

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Energy storage/utilization and reproductive condition were monitored in first and second year Long Island scallops held in cages between September 1984 and July 1985. Condition indices and proximate composition were determined for each tissue component.

Gonadal growth of first year scallops occurred in early spring at the expense of adductor muscle protein and lipid reserves. This contrasts with reported utilization of digestive gland reserves for reproduction in Massachusetts populations of the northern bay scallop. Carbohydrate utilization, commonly observed in other bivalves, was not apparent.

Histological analysis revealed that no residual, ripe oocytes remained in the gonads of older scallops by November. In March, first year and 80% of second year scallops were undergoing early gametogenesis. Twenty percent of the surviving, older cohort showed anomalous gonadal development, with the presence of ripe and resorbing oocytes. Mass senescent mortality of older scallops occurred before the period of gonadal buildup in early spring. This phenomenon does not appear to be associated with post-spawning energy depletion, nor with increased energy demand for a second reproductive event.

A three week starvation experiment at 15°C in January resulted in 4 and 38% mortality of first and second year scallops respectively. The two age classes showed different responses to starvation stress. Second year individuals exhibited significantly greater depletion of gonadal and mantle reserves than first year scallops.

EGG YOLK VESICLES AS A POTENTIAL FOOD SYSTEM FOR JUVENILE PACIFIC OYSTERS

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Vesicles prepared from egg yolk were shown to encapsulate protein and to be in a size range that would be filtered by the oyster. A radiotracer study involving addition of radiolabeled phosphatidylcholine to egg yolk demonstrated that the egg yolk vesicles were taken up and metabolized by juvenile *Crassostrea gigas*. Catabolism of the radiolabeled lipid and subsequent resynthesis into non-lipid components occurred to a slight extent. The main factor responsible for the distribution of radioactivity amongst the lipids in the stomach tissue was believed to be transacylation. The use of aspartate transcarbamylase as a potential indicator of growth will also be discussed.

REPRODUCTIVE BIOLOGY OF CLAM POPULATIONS IN NORTH AMERICA: A REVIEW

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Several generalizations can be made about those clam species which are cultured or have been recommended as candidates for aquaculture in North America. Most of the clam species are dioecious with *Mercenaria mercenaria*, a consecutive hermaphrodite, being the most notable exception. Dioecious species produce hermaphrodites approximately 0.1% of the time and exhibit a 1:1 sex ratio in most populations. Greater percentages of hermaphrodites and unequal sex ratios are more frequently encountered in stressful environments. Male clams tend to mature at a smaller size and younger age than females, one reason the sex ratio favors males in young uniformly-aged populations. Most species of clams mature by 3 years of age and before they reach 25% of their maximum size. Spawning cycles vary with latitude and ambient water temperature. Clams spawn on an annual or semiannual cycle during the warmer months; only *Tresus capax* and *T. nuttalli* spawn at the seasonal minimum water temperatures. Clams must achieve a certain degree of ripeness before they can respond to a spawning stimulus, and the key factor appears to be the spring water temperatures when gametogenesis occurs. Gametogenesis and spawning is orchestrated for maximum reproductive success. Fecundity is high and a costly expenditure of energy by clams.

GAMETOGENIC DEVELOPMENT OF THE VENERID CLAM *PROTOTHACA ASPERRIMA* IN THE BAY OF PANAMA

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Little is known about reproductive cycles of bivalve molluscs in the Bay of Panama. Although local coastal upwelling during the dry season (January–April) appears to significantly influence gametogenesis, the effect of the rainy season (April–December) on annual reproductive cycles is not known. Gametogenic development of the venerid clam *Protothaca asperrima* was studied as part of an ongoing hatchery development project for the production of commercially important bivalves. Adult clams used as broodstock were suspended in Japanese lantern nets in the Bay of Panama and were sampled biweekly for a period of one year. Gonadal development was determined histologically.

Preliminary observations of tissue sections from specimens collected during the rainy season indicate that spermaries remainin a ripened state and are continually replenished. Follicles were consistently observed to be either full or partially spent. Observations of simultaneous spawning and germinal activity were characterized by the presence of prominent bands or zones of spermatocytes and spermatids on the periphery of partially depeleted follicles.

Observations of ovaries during the rainy season indicate that female spawning activity is also continuous. In contrast to the male gonadal material studied, no evidence of fully ripened ovaries was found. Rather, follicles were observed to be partially, or in some cases, fully spent. Although gonadal replenishment or regeneration appeared to occur at a slower rate in females, there was extensive germinal cell activity with many oogonia observed forming on follicular membranes.

HOST RESPONSE TO *PROCTOECES MACULATUS* INFECTION IN THE BLUE MUSSEL, *MYTILUS EDULIS* L.

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Mytilus edulis from Ram Island Reef in Fishers Island Sound, Connecticut were sampled over a one year period. Prevalence of *Proctoeces maculatus* infection in and gonadal development of the host were determined histologically. The results showed that the development of *P. maculatus* was synchronized with the host reproductive cycle, that the mean prevalence of infection was 32.9 ± 3.50% and that in moderate to heavy infections, normal gametogenesis was either impaired or totally absent in 6 to 11% of the infected mussels. In addition, subtle effects of the infection manifested as delaying the early stage of gametogenesis and suppressing the number of mussels reaching the mature stage were also revealed.

Discharged sporosysts, free cercariae and adults elicited intense hemocytic infiltrations which were effective in destroying some of the parasite. Relevance of previously reported changes in the hemolymph biochemical constituents: carbohydrates, proteins and major free amino acids, will be discussed in terms of the infection and the gonadal development. Furthermore, ecological and genetic implications of the rediscovery of at least two distinctive reproductive patterns in Long Island Sound mussel populations will also be presented.

DEVELOPMENT OF ENZYME-LINKED IMMUNOSORBENT ASSAYS FOR DETECTION OF MOLLUSCAN PARASITES

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The detection of protozoan and metazoan parasites of commercially important molluscs is routinely done by expensive, time-consuming histological methods. A number of modern immunologic techniques are available, however, that might significantly reduce the time and expense of detecting parasites and, at the same time, provide valuable tools for basic research, including elucidation of life cycles.

We report here preliminary results of a project to develop an enzyme-linked immunosorbent assay (ELISA) for detection of the oyster parasite *Haplosporidium nelsoni* (MSX). We have had moderate success in isolating parasites from the hemolymph of oysters with advanced infections using velocity sedimentation with Percoll gradients. This method takes advantage of the fact that, on the average, plasmodial stages of MSX are larger (mean diameter 20 μm) than hemocytes (diameter 10 μm). Another source of (crude) antigen has been the blood and pericardial fluid of very heavily infected oysters ($>10^6$ plasmodia/ml) with high parasite-to-hemocyte ratios, used without further enrichment of MSX. Anti-sera to crude antigen have been raised in rabbits and mice using standard methods and tested with both fluorescent and enzyme conjugates. MSX gives an intense reaction with the fluorescent conjugate, indicating that it is highly antigenic and forecasting success with the use of more highly purified antigen to produce polyclonal antibodies or with the production of monoclonal antibodies.

EFFECTS OF MSX (*HAPLOSPORIDIUM NELSONI*) PARASITISM ON REPRODUCTION OF THE OYSTER, *CRASSOSTREA VIRGINICA*

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Besides causing heavy mortalities, the parasite *Haplosporidium nelsoni* (MSX) may inflict considerable sublethal damage to its host, the oyster *Crassostrea virginica*. A potentially very serious sublethal effect is that on reproductive success of populations in enzootic waters. We have analyzed tissue sections of nearly 2000 oysters collected during the oyster reproductive period in Delaware Bay, where MSX pressure is heavy. The object was to determine 1. the extent to which MSX interferes with gametogenesis, 2. whether it differentially affects males and females or alters sex ratios, and 3. whether there is a difference between the effect of MSX on reproduction of mortality-resistant oysters compared to mortality-susceptible oysters.

Results show that MSX parasitism significantly depresses gametogenesis in systemically infected oysters, but not in those with infections confined to the gills. Inhibition is proportional to infection severity, but affects males and females equally. There was evidence that infected oysters had a higher proportion of females than did uninfected oysters. Gametogenesis was significantly depressed in susceptible oysters with no patent infections and with advanced infections compared to mortality-resistant oysters in the same infection categories. There was no correlation between year-to-year fluctuations in MSX levels and spawning/setting patterns in Delaware Bay.

COMPARATIVE ANALYSES OF LARVAL AND EARLY POST-LARVAL SHELL MORPHOLOGY IN SEVEN MYTILID SPECIES

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The shell morphology of larval and early post-larval specimens is compared in seven mytilid species indigenous to the Atlantic Coast of North America. Mussels were spawned in the laboratory, and the resulting larvae were cultured through the early juvenile stage. Ontogenetic changes in shell morphology were documented with scanning electron photomicrographs of disarticulated valves.

Relationships of four quantitative features including the length and height of the shell, the number of provincular teeth, and the length of the provinculum vary among larval valves of the seven species. The practical value of these features for the discrimination of sympatric species is discussed.

Examination of the lateral hinge system facilitates distinction among juvenile mussels. Post-larval mytilids may have zero, one, two, or three types of marginal teeth. *Geukensia demissa* and *Amygdalum papyrium* lack marginal teeth. Only dysodont teeth are found in *Ischadium recurvum*, and only primary lateral teeth are found in *Modiolus modiolus*. *Mytilus edulis* has secondary lateral and dysodont teeth, and *Brachidontes exustus* has all three types of postlarval, marginal teeth.

STATUS OF COMMERCIAL SHELLFISH DEPURATION IN THE NORTHEAST-1986

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Currently, controlled purification (depuration) plants exist in three northeast states: Three soft clam plants and one hard clam plant in Maine; one soft clam plant in Massachusetts; and two soft clam and one hard clam plant in New Jersey. The plants range in age from four years to 58 years with six of the eight plants more than 10 years old. The plants use surface sea water, shallow salt water wells, and deep salt water wells. Some of the plants use flow through systems and some use recirculating systems. Each plant operates under authority given by state regulations. These plants were constructed under older regulations and concepts for the process, however few of the older concepts have changed since the plants were built. Because of the successful operation of the older commercial plants, there does not appear to be any great economic hardship.

PRELIMINARY STUDIES ON THE EFFECTS OF TIDAL CURRENTS, FOOD CONCENTRATION, AND SEDIMENT CHARACTERISTICS ON ONTOGENETIC GROWTH OF *MERCENARIA MERCENARIA*

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Water currents, food, and sediments are major environmental factors that affect growth rates of hard clams (*Mercenaria mercenaria*), but their relative effects are not well understood. Peterson et al. (J. Mar. Res. 42, 123–138, 1984) hypothesized that current velocity and food concentration interact so that the net effect depends on their relative strengths. The relation of sediment characteristics to these factors is not known.

Preliminary results from students at four sites in a coastal lagoon in southern New Jersey show that average growth rates of wild clams determined by examining annual bands in sectioned shells were (1) not correlated with near-bottom food concentrations estimated in 1985 by chlorophyll a and particulate organic matter; (2) positively correlated with near-bottom tidal current velocities, and "food provision rates" [FPR = current velocity converted to flow (e.g. l/s) × food concentration (e.g. mg/l) = biomass per unit time (e.g. mg/s)]; and (3) negatively correlated with sediment organic content. The slowest growth rates were at a fifth site affected by strong tidal currents that at times exceed critical entrainment velocities.

These results support Peterson et al.'s hypothesis, but they also suggest that at some point current velocity becomes inhibitory, and (in support of earlier reports) that sediment characteristics may be a factor. Additional studies including manipulative experiments are ongoing. It is suggested that in future work on growth of suspension feeders the effects of food concentration and water flow (or velocity) be determined using calculations of FPR, which may estimate the net effect of concurrent changes in both flow and food concentration.

A BIOENERGETIC MODEL OF JUVENILE DUNGENESS CRAB (*CANCER MAGISTER*) POPULATION DYNAMICS IN GRAYS HARBOR, WASHINGTON

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A bioenergetic model of juvenile Dungeness crab population dynamics has been developed to estimate assimilated energy required by a resident spring/summer population in Grays Harbor, a major west coast estuary. Principle parameters of the model are respiration at several temperatures (laboratory), population abundance and growth (both determined in the field).

Population respiration values were computed from crab weight/temperature relationships (0.03 to 30g; 6° to 18°C). The mean respiration for 10 mm carapace width (CW) intervals was determined based on average bottom temperature between two week sampling periods, and multiplied by the biomass calculated for that size interval throughout the estuary. Growth estimates were determined for four strata (areas) of Grays Harbor and for three moving age/size classes: 0+ (6–59 mm CW), 1+ (30–115 mm CW), and >1+ (77–160 mm CW).

Juvenile population abundance ranged from less than 1 million to over 20 million crab in constantly changing proportions of age class (size) and, therefore, biomass. The growth calculation includes energy as somatic growth and also energy lost as exuvia over each time interval. Population respiration and growth, as Kcal/ha, were summed over the estuarine strata and through the spring/summer in a cumulative estimate of energy assimilated by the juvenile crabs of Grays Harbor.

ASSESSMENT OF MORTALITIES IN SURF CLAMS (*SPISULA SOLIDISSIMA*) DUE TO DREDGING, SORTING AND DISCARD

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A significant portion of the clams available in the Mid Atlantic region are less than the current minimum legal size limit. Harvesters must either sort their catch and discard undersize clams, or modify their catch and discard undersize clams, or modify their gear so undersize clams will not be caught. Current harvesting practices cause significant mortalities to clams dredged, sorted, and returned to the sea.

To assess mortality associated with sorting and discard, clams were dredged and run through a mechanical sorter. Post sort "catch" (larger clams) and "discards" (smaller clams) were transplanted to marked plots at nearby areas. Plots were sampled with a hydraulic dredge and SCUBA divers 1, 24, 48, 72, and 144 hours after planting. Samples were sorted to determine percent mortality. To evaluate efficiency and effects of "bottom sorting" ie. increasing bar spacings in the dredge to allow smaller clams to pass through, divers sampled both inside and outside the path of a bottom sorting dredge fished through a dense population of undersize clams. Results of this study show that 1) with careful handling, minimal mortality to clams captured in a hydraulic clam dredge will average about 17–18% 2) sorting the dredged catch by steel rollers (current practice) adds another 18–19% kill 3) additional stress e.g. holding on deck, shovelling overboard etc. can add another 17–18% mortality. Predators increased in abundance and diversity in planting areas. A single tow evaluation of bottom sorting in this study confirmed high mortality rates reported by others in clams left behind in the dredge path (62% this study). This is a NJAES Publication No. K-32503-1-86, supported by federal funds.

THE DISTRIBUTION OF LARVAE OF THE BLUE MUSSEL *MYTILUS EDULIS* LINNE IN THREE MAINE ESTUARIES

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Water column abundance of blue mussel larvae as it related to tidal stage was investigated in three widely differing estuarine systems in Maine. A relatively wide coastal embayment, Webb Cove on Deer Isle, showed negligible differential position of larvae with tidal stage. The Damariscotta River, a 19-mile long, narrow drowned-river-mouth estuary, consistently produced enhancement of *Mytilus* (and *Mya arenaria* Linne) larvae by a factor of 3 to 5 on the flood tide. Minimum salinity (less than 1‰) and temperature (less than 1°C) changes occurred over the tidal cycle. A 3-mile long, narrow inlet, the Jordan River, in contrast, produced enhancement of larval and pelagic juvenile mussels by a factor of 35 on the flood tide. The effects of basin morphometry as it alters hydrography, particularly current velocity with resultant effects on larval distribution, is discussed.

THE SPATIAL DISTRIBUTION OF DUNGENESS CRAB (*CANCER MAGISTER* DANA) MEGALOPAE OFF THE WEST COAST OF VANCOUVER ISLAND, CANADA

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Relative abundance and spatial distribution of dungeness crab (*Cancer magister*) megalopae was monitored between March and August, 1985, along a transect line extending 180 km seaward off the west coast of Vancouver Island. Sampling for megalopae and newly settled crabs was also carried out in bays and estuaries around Tofino, B.C., from May through September, 1985. Megalopae was first collected offshore in April, reached peak abundance in June, and remained present to the end of sampling in late August. Neuston samples provided the best estimate of megalopae abundance. Inshore sampling indicated little crab settlement during 1985. Surface currents in the area of the transect line were northwest within 35 km offshore, but were predominantly southwest over the remainder of the continental shelf and slope. The boundary of these two currents shows properties of a convergence zone. Relatively large numbers of megalopae were found seaward of this boundary. This oceanographic regime is known to break down under certain meteorological conditions resulting in transport of surface water inshore. Hypotheses involving both large-scale and local oceanographic and meteorological events are proposed to explain the distribution of crab larvae and their settlement magnitude in inshore waters.

THE FORAGING BEHAVIOUR OF *CANCER MAGISTER* FEEDING ON *PROTOTHACA STAMINEA:* SIZE SELECTION AND RISK

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The foraging behaviour of the Dungeness crab, *Cancer magister*, was studied using optimal foraging theory. A model was constructed to predict optimal sizes of prey (*Protothaca staminea*) from values of energy content of the prey, energetic cost of feeding, and handling time. The model predicted that the larger sizes of prey were the most profitable. The predators preferred the smaller sizes of clams, considered unprofitable. These results can be explained with the use of energetic efficiency ratios (benefits/costs) and as a trade-off to minimize claw wear and the risk of claw breakage.

PUBLIC FISHERY AND PRIVATE MARICULTURE CONFLICT IN LONG ISLAND, N.Y.'s SHELLFISH INDUSTRY

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Long Island, N.Y.'s coastal waters support several commercial shellfish resources and are believed to have a high but unrealized potential for private shellfish mariculture. While many factors constrain mariculture development, the primary obstacle is the inability of private ventures to obtain exclusive use of suitable underwater levels; baymen who harvest natural shellfish stocks strongly oppose private mariculture and have successfully blocked every request made to or by government agencies for allocations of public lands for private mariculture use. Until this impasse is resolved, private mariculture will be severely limited.

The baymen have considerable political power and public support so that private mariculture will require at least their passive support. The benefits of private mariculture are considerable—it could be an important fishery management option while providing baymen with alternative employment and supplemental income. However, simply projecting benefits is insufficient to win baymen support. It is therefore first necessary to understand the basis of their opposition and then develop a private mariculture policy that addresses their concerns.

Baymen oppose private mariculture fearing loss of traditional freedoms, competitive disadvantages, and displacement by big business as well as a distrust of government regulators. Past and some current practices reveal these to be legitimate concerns. An acceptable mariculture program would therefore need the following attributes: accessibility by baymen and individuals, protection of the natural fishery limited scale, and strict oversight. These are not insurmountable and there is no reason why private mariculture cannot exist with commercial shellfishermen.

ASPECTS OF THE LIFE HISTORY OF THE PEA CRAB, *PINNOTHERES MACULATUS*

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In samples of the mussel, *Mytilus edulis*, collected over a fifteen month period from Ram Island Reef in eastern Long Island Sound, 98% contained the pea crab, *Pinnotheres maculatus*. Males and females were frequently found together in the same mussel except during summer months when females are ovigerous. A higher percentage of females than males was always observed.

To study the effect of tidal height on pea crabs two stocks of mussels of different sizes were used. The larger group, ranging between 6–8 cm in length, had a 98% prevalence of crabs while the other, ranging between 4–6 cm had a 10% prevalence. From September 1985 through January 1986, mussels were placed in cages and hung one foot off the bottom, one foot from the surface of mean high water (12 ft), and half-way between the two at the end of a dock. The results indicate an apparent attrition of crabs from mussels held at the high intertidal level. The larger mussels in the two deeper cages maintained the high prevalence of crabs. However, the smaller mussels experienced an increase in crab prevalence at the deeper depths in October, November and December and a sharp decrease in January. The apparent attrition of the crab is probably due to the fact that the smaller mussels were either physically or nutritionally unable to accomodate and support the growing crab when environmental conditions were unfavorable.

REPRODUCTIVE DEVELOPMENT IN THREE *MERCENARIA MERCENARIA* STOCKS GROWN IN SOUTH CAROLINA WATERS

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Juvenile *Mercenaria mercenaria* from Aquaculture Research Corporation in Dennis, Massachusetts (ARC), South Carolina wildstock (SCW) and a cross of the two were planted from July to October 1983 at a mean shell length of 8 mm. Beginning in July 1984, clams from each stock were collected monthly for a 14-month period. Clams were measured and gonads sectioned for histological examination. Binary coding based on developmental categories permitted analysis of variance by general linear model. Seventy-five percent of the clams in all three stocks had reached the differentiated stage by December 1984. Significant differences ($p < .05$) among spawning peaks were detected for the stocks and the interaction of month and stock. The ARC stock showed distinct spawning peaks in August and April, with a smaller peak in December while the SCW stock spawned only in July and March. Offspring of the ARC × SCW cross exhibited at intermediate spawning pattern.

UTILIZATION OF REFRACTORY CARBON BY THE RIBBED MUSSEL, *GEUKENSIA DEMISSA* (DILLWYN)

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The ribbed mussel, *Geukensia demissa*, is a common inhabitant of the intertidal region of east coast salt marshes. The ability of *G. demissa* to incorporate cellulosic carbon prepared from *Spartina alterniflora* was investigated with ^{14}C radiotracer techniques.

Spartina alterniflora was grown in an atmosphere enriched with $^{14}CO_2$. The refractory cellulosic component was then chemically extracted from the harvested plants. *G. demissa* were maintained in a 6 hour immersed: 6 hour emersed simulated tidal cycle for a 30 hour period. While immersed the mussels received marsh water, together with its natural complement of particulate material. The ^{14}C-cellulose was added to the marsh water only during the first 6 hours. Filtration, fecal deposition, pseudofecal deposition, respiration, and final body burden of ^{14}C were measured to assess how readily the material was digested and incorporated. The significance of cellulosic carbon in the marsh environment will be discussed.

USE OF DOWNWELLING CHAMBERS IN STUDIES WITH BIVALVE MOLLUSCS

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Flow-through chambers have been used by many researchers to study the feeding behaviour of bivalve mollusc species. The approach has many advantages over static systems. Resuspension of feces is avoided, particle concentrations can be maintained, low bacterial concentrations in the chamber can be achieved using filtered seawater, the animals can be rapidly exposed to various stimuli. We have designed and constructed a downwelling flow-through system for use in feeding studies with the oyster (*Crassostrea virginica*) and the mussel (*Mytilus edulis*).

Experiments indicated that the flow-through apparatus was especially useful in determining the effects of the ectoparasite *Boonea impressa* on the filtration rate of *C. virginica* because the experiments could be run for several days without the need to disturb the animals. Experiments have also been carried out to test the effects of dissolved substances from cultures of various algal species on the filtration rate of *M. edulis*.

Downwelling chambers have also been used in growth experiments with *C. virginica* fed on microencapsulated, artificial diets. Concentrations of bacteria were lower but growth of oysters poorer in downwelling chambers compared with those of animals in flask cultures.

DEPURATION: POLICY AND PRACTICE ON THE WEST COAST

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Recent closures of productive shellfish growing areas in some west coast states have generated an increased dialogue between the shellfish industry and state officials regarding depuration. Although there has been an increased interest in depuration, a major focus has been on the problems associated with the depuration alternative. There are currently no active depuration operations on the west coast and only California and Hawaii have had operations in the past.

The absence of depuration plants on the west coast is due more to industry resistance and the lack of need rather than state policy. Industry resistance is based on economic factors and the belief that depuration may reduce state efforts to clean up polluted growing areas. In addition, the west coast has not experienced growing area closures to the extent that some east coast areas have.

Although state policy on the west coast does not exclude depuration, only the State of Hawaii has adopted regulations on the practice. California has guidelines that will be incorporated into regulations in the near future.

ENERGY PARTITIONING PATTERNS IN CULTURED AND WILD POPULATIONS OF THE GIANT SCALLOP *PLACOPECTEN MAGELLANICUS*

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Growth rates of shell and somatic tissue plus quantities of energy invested in the production of gametes, soma and shell were determined for the giant scallop, *Placopecten magellanicus* from a population grown under conditions of suspended culture and a natural population in Newfoundland. Cultivated scallops displayed faster shell growth, heavier somatic weights, greater reproductive output and total production than wild scallops of equivalent age but placed less emphasis on shell production and displayed lower turnover ratios (P/B). Cultured scallops from this northern environment may reach marketable size in three years compared to four or five years required under natural conditions. In response to the somewhat artificial but better environmental conditions associated with suspended culture these scallops allocated proportionately more of their available energy to somatic growth resulting in lower estimates of reproductive effort. Potential consequences of the enhanced productivity observed in young cultivated scallops include reduced maximum size and shorter lifespan.

RECIRCULATION OF SEAWATER THROUGH UPWELLING SILOS IN A HARD CLAM NURSERY SYSTEM

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The potential for recirculating seawater through upwelling columns was investigated as a means of reducing costs of pumping seawater in a hard clam (*Mercenaria mercenaria*) nursery system. The need for high capacity pumps and associated costs of electricity and pump maintenance are significant expenses in the production of clam seed. Also, a greater flow is needed to force water uniformly through the bed of clams than is needed to meet food demands hence a single pass through upwelling columns may not be the most efficient use of pumped water.

Experiments conducted at The Clam Farm, Fisher's Island, NY, showed that under usual stocking densities chorophyll was removed and ammonia accumulated as seawater passed through consecutive tiers of upwelling columns. As much as 84% of ambient chlorophyll was removed in four passes through the system; ammonia levels increased by 86% after four passes. The rate of chlorophyll removal and ammonia accumulation generally was a function of clam biomass. There was evidence that a significant fraction of incoming phytoplankton was emoved from the water by purely mechanical means (trapped within the bed of clams) and not ingested. Growth in terms of total dry weight and ash-free dry weight declined significantly after more than two passes of water through the system. Individual variability in total dry weight and ash-free dry weight decreased as growth was limited with increasing water rouse. Increasing the efficiency of water recirculation in an upwelling system will depend on which factors (e.g., phytoplankton availability, ammonia accumulation) limit growth; several methods are discussed.

DISPERSAL OF BIVALVE LARVAE AT A FRONT IN THE JAMES RIVER ESTUARY, VIRGINIA

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The James River, Virginia, is the site of a major oyster fishery. Spawning of James River oysters usually occurs from June through September. We have examined the hypothesis that larvae swept downstream in surface waters on the southwestern side of the river are entrained in an anticlockwise gyre in the Hampton Roads region, and that these larvae are passively injected into deep, upstream flowing, highly-saline water at a pronounced frontal system which develops on flood tide. The distribution versus depth of bivalve larvae, including those of the oyster, was examined along a transect running perpendicular to the frontal system on three days in September 1985. Field observations were

supplemented with laboratory studies of oyster larval swimming behaviour in salinity gradients comparable to those present at the frontal system. Two questions are discussed: (1) what is the short-term (minutes-hours) influence of frontal activity on larval distribution, and (2) given that oyster larvae can swim in the vertical direction, what are the consequences of "deep injection" on long-term (hours-days) dispersal and retention of larvae in the James River?

IMPROVED STOCKS OF HARD CLAMS (*MERCENARIA* SPP.) THROUGH GENETIC MANIPULATION

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A large-scale breeding program in South Carolina utilizes genetic manipulation to improve growth and survival of hard clams. Three distinct breeding procedures are employed: induced heterozygosity, hybridization and selection. In the first year of this project, putative heterozygotes were produced by crossing selected strains from Aquaculture Research Corporation and Virginia Institute of Marine Science. The parents had been subjected to artificial selection for several generations and were assumed to be inbred, and therefore more homozygous than wildstock populations. Subsequent electrophoresis demonstrated that the parents are actually more heterozygous than wildstock, but some genetic drift has occurred. As a result, the offspring are distinct populations with genotypes differing from wildstock. Growth over the first year suggest that the outbred lines may have significantly improved growth rates. One outbred line averaged 35 mm in only 12 months from spawning, the fastest growth ever reported for hard clams. Electrophoretic analysis also suggested some interesting relations between specific enzyme loci and growth rate. Further electrophoresis is needed to clarify the results, but the possibility exists that typing parents before spawning and selecting for specific genomes can improve both survival and growth even further.

GENETIC IMPROVEMENT OF HARD CLAM, *MERCENARIA* SPP., POPULATIONS FOR COMMERCIAL MARICULTURE STOCK DEVELOPMENT IN SOUTH CAROLINA

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A cooperative project involving four research institutions is performing genetic manipulation to produce stocks of hard clams suitable for commercial mariculture and the restoration and/or enhancement of wildstock populations. Modifications of existing clam stocks are accomplished by three distinct breeding procedures: induction of heterozygosity, selection, and hybridization. Constructed populations are studied to assess the relationship between reproductive activity and somatic growth. Larval studies are conducted to determine gamete compatibility, survival of different strains under different culture conditions, differences in larval morphometrics, and egg size/survival relationships. Protein electrophoresis is used to assess relationships between heterozygosity and growth, determine allozyme/loci correlations with growth, and assess variations in detected effects throughout the life cycle. Rates of net energy gain under different environmental conditions are determined for produced strains to establish genotype/environmental interactions affecting growth. In the first two years of this long-term project, all three breeding strategies have been addressed, electrophoresis has been completed on parents used to induce heterozygosity and on two groups of offspring, and gametogenesis and fecundity analyses have been performed on existing populations from South Carolina and Massachusetts.

DIURNAL VERTICAL DISTRIBUTION AND DISPERSAL-RECRUITMENT MECHANISMS OF DECAPOD CRUSTACEAN LARVAE AND POSTLARVAE IN THE CHESAPEAKE BAY, VIRGINIA AND ADJACENT OFFSHORE WATERS

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The diurnal vertical distribution of decapod larvae and postlarvae was studied from late-summer samples collected at three stations: York River mouth (estuarine) (37°12′N, 76°16′W), Chesapeake Bay mouth (transition) (36°58′N, 76°07′W), Chesapeake light tower (offshore) (35°54′N, 75°43′W). Each station was occupied for a continuous 72 hour period, and quantitative plankton samples were taken every three hours from the following depths: neuston (0.10–0.15 m), 1 m, 3 m, 6 m and epibenthic (11–13 m). A total of 41 species, 160 developmental stages and an estimated 6,000,000 specimens were obtained. *Callinectes sapidus* accounted for 87% of the total collection followed by *Uca* spp. (3%), *Pinnixa chaetopterana* (2%) and *Hexapanopeus angustifrons* (1%). Results indicated that spatial proximity to the estuary greatly affects vertical positioning. Light was proposed to be the major factor influencing distribution, with no significant effects from tidal cycles or other environmental factors. Six dispersal-recruitment patterns were established based on vertical and spatial distributions and adult habitats: retained estuarine (*Neopanope, Palaemonetes, Panopeus*), retained estuarine-transitional (*Callianassa, Pinnixa, Pinnotheres, Upogebia*), retained transitional-nearshore (*Euceramus, Hexapanopeus, Pagurus*), retained offshore (*Emerita, Libinia, Ovalipes*), expelled with estuarine spawning (*Uca*) and expelled with transitional spawning (*Callinectes*). Dispersal-recruitment mechanisms consisted of maintenance at a given depth, active vertical migration and migration to a depth of no net motion. Fluctuations in dispersal and recruitment greatly affect adult populations ecologically or economically, and vertical distribution plays an important role in these processes. This work was partially supported by the Office of Sea Grant, NOAA.

SPACIAL AND TEMPORAL VARIABILITY OF DECAPOD LARVAL DISTRIBUTIONS AS REGULATING FACTORS IN ESTUARINE DECAPOD POPULATIONS DYNAMICS

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Variations in spacial and temporal distribution of decapod larvae can alter transport and recruitment success. Interannual and seasonal variability in the physical driving forces associated with planktonic larval transport can result in spacial distributions that either enhance or restrict larval recruitment to the adult habitat. Temporal variability in spawning or larval developmental rate may alter recruitment success and juvenile growth rates between year classes. For species such as *Callinectes sapidus* and *Uca sp.* that spawn in the lower reaches of the estuary and develop offshore, these factors are especially critical.

Based on extensive distribution studies in the lower Chesapeake Bay and adjacent shelf region, we have developed conceptual models of the spacial variability on larval transport and recruitment of ecologically and commercially important decapod species. These models include the role of spacial distribution on both density dependant and independant variables. The models suggest that there are two major shelf-estuarine transport and recruitment strategies, inner shelf retention and cross shelf transport. Both require different spacial distributions for optimal recruitment success.

This work was supported in part by grants from NOAA, Office of Sea Grant and the Virginia Sea Grant Program.

INTERTIDAL DISTRIBUTION AND ABUNDANCE OF YOUNG-OF-THE-YEAR DUNGENESS CRAB *CANCER MAGISTER* IN NORTHERN INLAND WATERS OF WASHINGTON

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The inland waters of the State of Washington support a substantial sport and commercial fishery for Dungeness crab *Cancer magister*. Recently the importance of shallow, nearshore and estuarine habitat as nursery areas has been shown for coastal crab stocks. Within the northern Puget Sound region, concern for this potentially critical habitat is growing in light of continuing and increasing pressure to develop or otherwise degrade these areas.

The North Puget Sound Crab Habitat Study has focused on areas which support the major portion of the inland crab harvest. Intertidal sampling for Young-of-the-Year (YOY) Dungeness crab was conducted over 18 months at Semiahmoo Spit, Birch Bay, Lummi Bay, Padilla Bay and Dungeness Spit.

The greatest mean densities of YOY crab occur where plant cover is present (mean density; 3.18 crab/m^2), but densities vary in accord with plant species and percent vegetative cover. Where plant cover is absent (mean density; 0.85 crab/m^2), abundance is associated with substrate particle size. Silt and sand substrates

support fewer crab than substrates of gravel, cobble and/or broken shell material.

The availability of suitable habitat to early postlarval Dungeness crab may play an important role in successful year class recruitment. The quantity and quality of habitat available also has implications in possible mitigative or enhancement measures as means to reduce project impacts on the species.

RESPONSES OF *GEUKENSIA DEMISSA* TO DISSOLVED COPPER AT VARIOUS SALINITIES

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The uptake of copper by mollusks, and its ultimate toxicity are greatly affected by salinity. Toxic effects of copper are synergystically enhanced by salinity departures from the physiological optimum for the species. One possible explanation is a reduced efficiency in the production of metallothionein-like metal-binding protein (MT) during salinity stress. A series of laboratory experiments were performed to evaluate salinity effects on the toxicity of copper to the euryhaline ribbed mussel, *Guekensia demissa*, and the relationship between physiological response and binding of copper to MT.

High and low salinity populations of mussels were placed in aquaria at 10 and 30 ppt salinity for a 4 day acclimination period. Mussels were then exposed to 75 ppb copper for seven days, followed by a 7 day depuration period. Copper accumulation, byssal attachment, and binding of copper to metallothionein-like protein were monitored throughout.

There were significant losses of byssal attachment in both populations at both salinities during copper exposure, resulting in less than 20% attached after the 7 day exposure. Although uptake of copper at 30 ppt was less than at 10 ppt, mussels from both populations at 30 ppt did not recover byssal attachment during the depuration period. This is in contrast to both populations of mussels at 10 ppt where rapid and complete recovery took place. Binding of copper to MT occurred in high and low salinities. Mussels at 30 ppt has more copper bound at MT then at 10 ppt, suggesting that toxic effects of Cu were enhanced by high salinity.

THRESHOLD LEVELS OF CRAB CHEMORECEPTION FOR AMINO ACIDS AND RESULTS OF FIELD TESTS USING THESE AMINO ACIDS AS ATTRACTANTS IN ARTIFICIAL BAIT

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Various amino acids were tested on *Callinectes sapidus* and *Cancer irroratus* to determine threshold levels of chemorception. Molarities were detected by *C. sapidus* as low as 10^{-12}. However, *C. irroratus* demonstrated even greater chemosensitivity which may allow them to utilize darker and therefore deeper habitats than *C. sapidus*.

Some of these amino acids were used as chemical attractants in artificial bait for *C. sapidus*. The artificial baits were not as effective as natural bait on the first day but were nearly as effective on day two.

A REVIEW OF INFECTIOUS DISEASES OF THE DUNGENESS CRAB, *CANCER MAGISTER*

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A baseline survey to investigate the infectious diseases of Puget Sound Dungeness crabs, *Cancer magister*, near Mukilteo, WA was initiated in late 1977. Our survey has since expanded to include the inland and coastal waters of Washington state and southeast Alaska.

A disease of potentially significant importance is one caused by a chlamydia-like organism. The microbe was found in 3 of 14 (21%) Dungeness crabs captured in Feb., 1979 from Willapa Bay, WA, during reported mortalities. The organism was subsequently found in crabs from Mukilteo, captured and processed but not examined prior to the epizootic. All diseased Dungeness crabs have been found between the months of December and March, the highest prevalence (13%, 6/84) occurred during the period of the reported high mortalities.

Other diseases found during our survey include a microsporidian (Family Nosematidae) infection of skeletal muscle, a systemic ciliate (Paranophrys sp.) infection, and trematode metacercariae in the nervous and connective tissue of *C. magister*. The prevalences and distributions of these diseases will be presented and their possible impact on the fisheries will be discussed.

DIGESTION AND ABSORPTION OF REFRACTORY CARBON BY THE OYSTER, *CRASSOSTREA VIRGINICA* (GMELIN).

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The role of refractory detrital material in the nutrition of oysters has been the subject of some debate. Results from stable isotope ratio analysis indicate that the oyster, *Crassostrea virginica*, derives negligible amounts of carbon from *Spartina alterniflora* detritus. Higher estimates (up to 40% of the total carbon requirement) have been inferred from *in vitro* measurement of style cellulase activity.

We have grown ^{14}C labelled *S. alterniflora* and removed the labile organic compunds to produce a defined source of refractory detritus. This labelled material was fed to groups of oysters that were maintained in filtered seawater. Some groups were treated with the antibiotics chloramphenicol and rifampicin added at 5mg/l to the seawater. Direct counts (DAPI) of bacteria demonstrated that treatment with antibiotics eliminated bacteria from the oyster's stomach fluid.

After 24h the ^{14}C specific activities of cell-free hemolymph and tissue samples indicated that oysters were only able to digest and absorb 1.3% of the carbon from the *S. alterniflora* material. There were no significant differences (ANOVA $p > 0.05$) in the digestion and absorption of ^{14}C material between antibiotic treated and untreated oysters. These results indicate that oysters are only able to digest small amounts of refractory cellulose and that this process is not enhanced by bacteria in the stomach. We estimate that oysters living in Chesapeake Bay are able to meet only 4% of their total carbon requirements from direct utilization of refractory carbon.

RECRUITMENT OF BLUE CRAB, *CALLINECTES SAPIDUS*, IN OPEN AND IMPOUNDED MARSH SYSTEMS IN SOUTH CAROLINA

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Macroplankton samples were collected January 1983—January 1984 to investigate patterns of recruitment of blue crab (*Callinectes sapidus*) in open and impounded salt-marsh in South Carolina.

In the open marsh (*Spartina*) system, initial recruitment of blue crab appeared to be predominately by megalopae. Megalopae were collected May–December, with major ingress into the marsh September–November, at which time densities of megalopae reached 3.9/m^3. Recently metamorphosed juveniles also were collected from the plankton. Densities of blue crab megalopae during flood exceeded those during ebb by a factor of five, indicating directed movement into the marsh. Megalopae also were collected in greater densities at night than during day.

Patterns of recruitment of *C. sapidus* in impoundments differed from those in the open marsh, largely because of reduced water flow into impoundments during the period of megalopal abundance. Movement of blue crabs into impoundments was mostly by juveniles (>8 mm TW), with maximum recruitment in May.

THE SETTING PATTERNS OF THE PURPLE-HINGE ROCK SCALLOP, *HINNITES MULTIRUGOSUS* IN HUMBOLDT COUNTY, CALIFORNIA

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The setting of the purple-hinge rock scallop, *Hinnities multirugosus*, was monitored in 1983 and 1984 in Humboldt and Trinidad Bays, California. Onion bags filled with used gill net were used as collectors and these were suspended from rafts at both sites during the setting season.

The setting season in Humboldt Bay began in June and lasted until early November. The number of spat per collector was low and not of sufficient numbers to collect commercially. In Trinidad Bay, the setting season was shorter (July through early October). Here setting was of commercial significance. Over 4,000 scallop spat were found on one collector that was in the water from June 27 to September 7, 1984. Others suspended during this period had from 1,000 to 3,000 per collector.

Of interest was the number of mussels, *Mytilus edulis*, that were found on the collectors in Trinidad Bay. One collector had over 50,000 mussel spat while several others varied from 20,000 to 40,000 spat per collector.

The advantages and disadvantages of attempting to collect either scallop or mussel seed in Northern California are discussed.

TEMPORAL VARIATION IN GROWTH RATE, BODY AND GONAD WEIGHT IN A POPULATION OF *MYTILUS EDULIS* IN THE SANTA BARBARA CHANNEL

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This study examined relationships between temporal variation in growth rate, body and gonad weight of *Mytilus edulis* and variation in water temperature and chlorophyll *a* concentration at an oil production platform located 3 km offshore of Goleta, California. To measure temporal variation in growth rate, populations of 20 mm length mussels were enclosed monthly in cages at a depth of 2 m and bimonthly at depths of 9 m and 18 m. The mussels were numbered and measured prior to enclosure and measured thereafter every 3–4 weeks. Growth rate of 20 mm mussels varied over time ranging from a low of 5.5 mm/mo in December 1984 to a high of >9.0 mm/mo in late May 1985. Mussels grew from 20 to 50 mm in 3.7 to 7.0 mos. Growth rate was greatest at a depth of 9 m. Growth rates estimated from population samples agreed with data from caged populations. Dry weight of somatic and gonad tissues, measured approximately monthly for 72 mm mussels, varied over time. Somatic weight ranged from a low of 0.8 g in December to a high of 2.3 g in August. Gonad weight ranged from <0.1 g in February to 2.0 g in August. Water temperature and chlorophyll *a* concentration were measured weekly beginning in early 1985 at depths of 2 m, 9 m and 18 m. Water temperatures ranged from a low of 11 C in Winter and Spring to a high of 18 C in Summer and Fall. Chlorophyll *a* concentration varied from 0.2 μg/l in the Fall to >8.0 μg/l during a Spring "bloom." Temporal variation in growth rate was positively associated with variation in chlorophyll *a* levels, but not water temperature. The results indicated that growth, reproduction, and nutritional condition of *M. edulis* may be enhanced in the area of higher phytoplankton biomass near Pt. Conception, California (45 km north of Santa Barbara).

A RELATIONSHIP BETWEEN SELECTIVE LARVAL SETTLEMENT AND ADULT DISTRIBUTION PATTERNS OF GEODUCK CLAMS AND THE PRESENCE OF CHAETOPTERID POLYCHAETE TUBE MATS IN PUGET SOUND, WASHINGTON

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Visual observations during subtidal diver survey of geoduck clam *Panope abrupta* beds revealed that epibenthic mats of intertwined tubes of the chaetopterid polychaete species *Spiochaetopterus costarum* and *Phyllochaetopterus prolifica* commonly occur with geoduck clams in Puget Sound. We demonstrated that of 56 macrofauna species commonly observed during subtidal surveys, the chaetopterid polychaetes *S. costarum* and *P. prolifica* co-occurred with geoduck clams more frequently than any other species. The density of geoduck clams was significantly higher in transects where the chaetopterid polychaetes occurred. We showed that competent geoduck clam larvae metamorphosed in response to tubes of the polychaete species *S. costarum*, *P. prolifica* and *Diopatra ornata*, but not in response to tubes of *Onuphis elegans*. We demonstrated that competent geoduck clam larvae respond to chemicals from the precipitate and supernate of a seawater extract of *S. costarum* and to the amino acid L-Dopa. Our findings suggest that the epibenthic mat of tubes formed by the polychaetes *S. costarum*, *P. prolifica*, and *D. ornata* in Puget Sound identify a habitat where the probability of survival of recruiting geoduck clams is increased. We further suggest that adult geoduck distribution patterns reflect selective larval settlement into a biological refuge (i.e. the polychaete tube complex) which occurs in a habitat suitable for adult geoducks.

SHORT-TERM AND LONG-TERM SETTLEMENT OF LARVAL AND JUVENILE *MYTILUS EDULIS L.*

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The settlement of larval and juvenile mussels was examined over consecutive tide cycles on July 9–10 1984 (short-term) and weekly or biweekly from May to October 1984 (long-term). Experiments were carried out in a small, shallow embayment, Webb Cove, Stonington, Maine. Short-term settlement of larvae and juveniles off the bottom was greatest at mid-ebb and mid-flood. Larval set was concentrated in the middle of the water column (three and four meters) while juvenile set was greatest at both the surface and middle of the water column (one to four meters). Recruitment into the water column is probably the result of setting larvae and juveniles being swept off the bottom during periods of increased current velocity. Long-term settlement patterns indicate that settlement is dominated by primary (larval) set in June and most of July. Juvenile settlement becomes important in mid July and remains relatively dominant through October. Results of both short and long-term experiments indicate that juvenile settlement is common and may lead to a significant redistribution larval set.

SMALL-SCALE SPATIAL DISTRIBUTION OF OYSTERS (*CRASSOSTREA VIRGINICA*) ON OYSTER REEFS

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The small-scale spatial distribution of oysters was examined on 11 reefs in the Copano Bay—Aransas Bay area of the Texas coast. Small oysters ($\leq$2 cm) were contagiously distributed ($s^2/\bar{x} > 1$) and positively spatially autocorrelated. Patch size ranged up to about 40 cm. Large oysters ($>$ 5 cm) were less contagiously distributed and normally were negatively spatially autocorrelated. Negative spatial autocorrelation was restricted to adjacent clumps $<$12 cm apart. Consequently, as the oyster populations aged, their spatial distributions changed. The spatial distribution of large oysters on nearly clumps was affected by the number of large oysters distributed among the clumps. As the variance-to-mean ratio increased, the populations became more negatively spatially autocorrelated. Consequently, large oysters affected the survivorship of oysters on adjacent clumps. Mortality, produced perhaps by predation and disease, modulated by competition for food affecting the oyster's suseeptibility to mortality, could explain these changes in distributional pattern.

DEVELOPMENT OF EPIBENTHIC FOULING COMMUNITIES ON SHELLS DEPOSITED ON A NATURAL OYSTER BED IN THE JAMES RIVER OF VIRGINIA

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The development of fouling communities on oyster shells deposited on a natural bed of the oyster (*Crassostrea virginica*) in the James River, Virginia was followed over a 19 week period. Clean shells were placed on an oyster bed on four sequential dates at two week intervals, beginning on May 21. Shell samples were collected from each of the four groups at two week intervals and the relative coverage determined for biotic and abiotic fouling components. A detrended correspondence analysis ordination was used to depict changing patterns of community composition over time.

All four shell groups exhibited a rapid increase in fouling coverage which peaked at the period of maximum water temperature in mid-August. The primary fouling components were nonliving (sediment and detritus) and contributed to approximately 40–45% of the peak coverage. Attached sessile organisms contributed to an additional 15–20% of the coverage.

The initial species dominants for each of the four shell groups reflected seasonal setting patterns, however, the four shell groups converged in their community composition over time. It appears that a substrate destabilization process (probably biologically caused) affects the composition of a seasonally changing climax community, the composition of which is ultimately regulated by seasonal water temperature fluctuations.

At the peak in oyster set near July 15, there was no significant difference in the densities of oyster set on the shells of the four shell plantings.

INTERSTATE SHIPMENT OF LARVAL AND JUVENILE BIVALVES: EFFECTS OF SHIPPING DURATION AND METHOD ON SURVIVAL

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Survival of bivalve larvae and seed during shipment has been of interest to mollusk culturists for many years. The present study was designed to determine the effects of shipping method (air & surface) and duration on survival of two species of bivalve mollusks, the hard clam, *Mercenaria mercenaria*, and the bay scallop, *Argopecten irradians*. Larvae, postset, small seed (~1.0 mm) and young juveniles (~5.0 mm) of both species were shipped between Charleston, South Carolina and Milford, Connecticut by both overnight air and regular surface delivery. A contrived schedule of packing and shipping allowed shipping durations to range from as short as 24 hours to as long as six days. Identical seafood shipping containers (styrofoam coolers with corrigated cardboard outer boxes) were used in all shipments from both locations and each container held two replicates of each bivalve size.

Results showed a direct correlation between shipping duration and mortality of bivalve seed. There was also a clear relationship between seed size and mortality in shipment. The greatest mortalities occurred in the smallest size bivalves shipped over the longest

period of time. The highest survivals were recorded in the largest size bivalves shipped over the shortest period. Larvae and postset exhibited appreciable mortalities in shipment durations longer than 24 hours. In general hard clams exhibited greater overall survival than scallops at almost all size classes and shipping durations.

ECONOMICS OF SHORESIDE DEPURATION

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The controlled purification of bacteriologically contaminated shellfish through depuration has become a controversial but acceptable technology for increasing molluscan production in the United States. Using secondary and primary data sources, information on South Carolina hard clam (*Mercenaria mercenaria*) plants' costs and returns were compiled. Typical initial investment, operating costs and revenues of these plants was generated using microcomputer software. Factors affecting "start-up" costs and operating expenses include tank sizes, sea-water sources, availability of hard clam stocks and depuration regulations.

Hard clam depuration costs were extrapolated to the shoreside depuration of the eastern oyster (*Crassostrea virginica*). The effects of quantities processed and wholesale prices were analyzed for oyster depuration using a U.V. light system. The simulation of depuration plant financial performance should enhance both private sector feasibility studies and public sector policy analysis (e.g. impact of increasing user fees, shellfish relaying, costs and benefits of water pollution mitigation, etc.).

DEVELOPMENT OF TECHNOLOGY FOR HARVESTING AND TRANSPLANTING SUBTIDAL JUVENILE PACIFIC RAZOR CLAMS, *SILIQUA PATULA* DIXON, ALONG THE COAST OF WASHINGTON STATE

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In 1979, the Washington Department of Fisheries initiated a research project to determine the feasibility of enhancing the unstable and heavily exploited harvestable populations of intertidal Pacific razor clams, *Siliqua patula* Dixon, along the Washington coastal beaches by harvesting subtidal seed clams and transplanting them to sparsely populated intertidal locations. Early technological development centered around two independent mechanical harvesting systems: a small hydraulic surf clam harvester and a small sled mounted airlift harvester. Because the harvesters were towed by a Department patrol vessel, the systems had to be portable and were extremely cumbersome and labor intensive. A subsequent evaluation of the project's technical capabilities combined the excavating efficiency of the hydraulic harvester and the sorting capacity of the airlift harvester to produce a mechanical hydraulic-airlift harvesting system. The excessive speed of the towing vessel and the logistic limitations inherent with the portable nature of the equipment were overcome by integrating them with a sophisticated support system aboard a research vessel outfitted to meet project specifications. The potential of this integrated harvesting system was demonstrated during the summer and early fall of 1985 when over 125 million juvenile razor clams were harvested from a subtidal area northwest of Copalis Beach, Washington. More than 90 million of these were successfully transplanted intertidally to Washington's Twin Harbors Beach and the Long Beach Peninsula.

ASPECTS OF THE EARLY SUBTIDAL LIFE HISTORY OF THE PACIFIC RAZOR CLAM, *SILIQUA PATULA* DIXON, OFF THE COAST OF WASHINGTON STATE

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In early August of 1985, the Washington Department of Fisheries discovered an extremely large subtidal population of juvenile Pacific razor clams, *Siliqua patula* Dixon, off the Washington coast. A systematic survey of the subtidal habitat off the south central coast of Washington with the mechanical hydraulic-airlift juvenile razor clam harvester, indicated that the area of greatest abundance was centered 4.8 kilometers northwest of Copalis Beach, Washington. During an eight day period in August and September, 45 tows were concentrated in this 5.0 square kilometer area, at depths ranging from 1.5 to 13.7 meters below mean lower low water (MLLW). Abundance of juvenile razor clams within these confines was conservatively estimated at 28 billion.

Density of juveniles was demonstrated to vary directly with increasing depth and inversely with mean size. At 12.2 meters below MLLW, the size composition of clams was very homogeneous with a 2.0 millimeter mean size. At this depth, juvenile density was a maximum of 38,000 clams per square meter. At 1.5

meters below MLLW, size composition was heterogeneous, with the mean size ranging between 8.0 and 12.0 millimeters. Juvenile clam density at this depth was a minimum of 37.0 clams per square meter. These results although preliminary, appear to support the hypothesis that settlement of post metamorphosed larval *Siliqua patula* occurs subtidally at very high densities. Subsequent intertidal settlement of juveniles at lower densities, is hypothesized to be the result of a mechanism involving growth, movement and mortality.

BACTERIAL AND VIRAL ELIMINATION IN COMMERCIAL PLANTS

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Shellfish such as oysters and clams are filter-feeding organisms and can accumulate under optimal conditions pathogenic bacteria and virus at concentrations several fold greater than their ambient seawater environment. If such shellfish are consumed raw and/or improperly cooked, they may represent a risk for bacterial and viral illness. For these reasons, interest in controlled cleansing (-depuration) of shellfish has increased.

Methods for depurating contaminated shellfish involves the holding of shellfish in recirculating seawater treated with: (1) ultraviolet light; (2) ozone; and (3) chlorine. In addition, the relaying of polluted shellfish to non-polluted waters has been utilized as a method of depuration.

Each of the above mentioned method will be discussed. Emphasis will be given to factors that influence the rates of uptake, retention and the elimination of bacteria and virus in both oysters and clams.

(Supported in part by funding from Florida Sea Grant and NOAA)

EXPERIMENTAL PRODUCTION OF GYNOGENETIC AND PARTHENOGENETIC *MULINIA LATERALIS* (SAY)

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The rapidly maturing dwarf surf clam *Mulinia lateralis* (Say), an ideal organism for developing a system directed toward producing pure-breeding lines for breeding programs in the more slowly maturing commercially recognized species such as oysters and clams, was used to produce gynogenetic and parthenogenetic zygotes. Efficient procedures for producing these forms were established and developmental processes were monitored with the aid of a DNA specific fluorochrome and epifluorescence microscopy.

Combinations of an activating agent ('normal' sperm, potassium ions, or UV-irradiated sperm) with or without the addition of cytochalasin B, at critical times in the development sequence, were used to produce diploid, triploid, tetraploid, parthenogenetic haploid, parthenogenetic heterozygous diploid, gynogenetic haploid, gynogenetic heterozygous diploid, or gynogenetic homozygous diploid zygotes. Parthenogenetic haploid and parthenogenetic heterozygous diploid zygotes did not develop past the one-cell stage. Diploid, triploid, tetraploid, and gynogenetic haploid zygotes developed to D-stage larvae, whereas gynogenetic diploid animal development was abnormal and arrested before the D-stage was reached. The non-viability and abnormal development of gynogenetic diploid zygotes may be a result of; 1) the expression of lethal recessive genes due to high level of homozygosity, 2) missing paternal genes that mediate maternal gene expression, 3) an unknown cytochalasin B effect on cellular processes, or 4) a missing biochemical intermediate which could be supplied by an exogenous source.

A PROPOSED STANDARDIZATION OF THE STAGES IN THE GAMETOGENESIS CYCLES OF BIVALVES

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Papers describing the gametogenesis cycle of bivalves were examined. There was an apparent lack of consistency in describing the gonadal stages in these papers, thus making comparisons difficult. It is suggested that the stages be standardized as follows: active, ripe, partially spawned, and spent. In some instances there could be a fifth stage, e.g. indifferent, summer, inactive. Several cycles will be presented to demonstrate the use of the proposed stages.

THE EFFECTS OF THE TOXIC DINOFLAGELLATE, *PROTOGONYAULAX TAMARENSIS*, ON THE PHYSIOLOGY AND BEHAVIOR OF MARINE MOLLUSCS

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Filter feeding bivalve molluscs accumulate poisons from toxic dinoflagellates such as *Protogonyaulax tamarensis* during feeding. In spite of a number of references to the contrary, it is still stated quite frequently and usually dogmatically that dinoflagellate toxins have no effect(s) on the general well-being of the host bivalve molluscs. In light of the high toxicity of dinoflagellates and the apparently conflicting views on this subject, a number of experiments were carried out using commonly occurring bivalve species of the Gulf of Maine. In the presence of *Protogonyaulax tamarensis*, molluscan responses are species-specific and various combinations of the following responses are seen in individual species: shell valve activity is altered; oxygen consumption rates increase/decrease; heart rates become erratic; byssus production in mussels is reduced and a reduction in feeding rate may occur. In addition, differences were noted between populations of mussels from 'red-tide' and 'non-red-tide' areas indicating a possible adaptive mechanism(s).

USE OF DISPERSION MODELS FOR PREDICTION OF BIVALVE LARVAL RECRUITMENT

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In support of efforts to manage Long Island's economically important fisheries for the hard clam (*Mercenaria mercenaria*) and the bay scallop (*Argopecten irradians*), computer models calibrated against hydrographic data have been developed to predict distribution of larvae in the Great South Bay and the Peconic Bays Estuary. The goal of the research in Great South Bay was to evaluate the potential contributions to recruitment from populations of hard clams in uncertified waters and in man-made "spawner sanctuaries." This quantitative evaluation required the simulation of advective and diffusive dispersal of particles whose number was reduced over time to simulate larval survival. Results of the model forecast locations of maximum recruitment from chosen sanctuary sites. Town shellfish management programs have created spawner sanctuaries at sites predicted to result in maximum recruitment in areas favorable for growth and survival. The goal of the modelling for the Peconic Bays Estuary was to predict sites for spawner sanctuaries of bay scallops which will be created to help rebuild scallop populations following an apparent failure of natural recruitment caused by an extraordinary diatom bloom in 1985. This more qualitative evaluation of recruitment required forecasting the dispersal of larvae from proposed spawner sanctuaries and hindcasting the locations of spawning stocks whose larvae recruit to areas favorable for growth and survival. The utility of this modelling approach in shellfish management is discussed in view of the physical and biological assumptions inherent in the models.

OVERVIEW OF NMFS SHELLFISH DEPURATION RESEARCH

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Researchers within the National Marine Fisheries Service are conducting studies on cost-effective removal of enteric viruses, toxic metals, and paralytic shellfish poison at our Charleston, S.C., and Milford, CT laboratories. Improved techniques are being developed for cell culture-based assay of Norwalf and Hepatitis A viruses using attenuated Polio virus as a reference for the extraction procedures. Further, samples are being analyzed following commercial-scale depuration for fecal coliform, *E. coli*, and enterovirus (Polio, Echovirus, and Coxsackie types A&B viruses) concentrations. High salinity, high temperature, and high concentrations of dissolved organics compose optimal conditions for the elimination of cadmium by eastern oysters. However, conditions have not been identified that will allow cost-effective removal of cadmium and other metals in short-term shore-based depuration facilities. Application of ozone for depuration of disease-causing organisms is difficult for the removal of Vibrio species but is very effective for inactivating paralytic shellfish poison.

SPATIAL AND TEMPORAL VARIATION IN THE ABUNDANCE OF MALE AND FEMALE DUNGENESS CRABS (*CANCER MAGISTER*) NEAR TOFINO, B.C., WITH IMPLICATIONS FOR THE COMMERCIAL FISHERY

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Dungeness crabs (*Cancer magister*) near Tofino, British Columbia have been sampled monthly since May 1985 using a beam trawl (for smaller crabs) and traps (for larger crabs). Fishing locations, intensity and success of local fishermen have also been monitored. Beam trawl results indicate that abundance of 2–3 year-old crabs is highly variable among selected locations in the local archipelago. The same cohort was never caught in abundance on the open coast. In one location we observed a particularly high concentration of both sexes. In a second location, with a more direct access to the open coast, we observed two separate concentrations; one dominated by males, the other by females. Our data suggest that, where feasible, movement of males and females to preferred habitats may occur. There are productive commercial fisheries for older males where we found high concentrations of 2–3 year-old males.

A FIELD TEST OF THE AMERICAN OYSTER HABITAT SUITABILITY (HSI) MODEL

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The HSI model, developed by Cake (1983) for the American oyster, has been field tested on 38 0.1 hectare reef and non-reef sites in Galveston Bay. The HSI is dependent upon six (HSI1) or optionally, eight variables (HSI2). The variables of the model are percent of bottom covered with suitable cultch, mean summer water salinity, mean abundance of living oysters (a gregarious settling factor), historic mean water salinity, frequency of killing floods and substrate firmness. The optional variables are density of southern oyster drills and intensity of *Perkinsus marinus*. The HSI1 values of reef and nonreef sites are significantly different (Wilcoxon 2-sample test, $p < 0.0001$) and the model is capable of distinguishing where oysters are found from areas where they are absent. HSI1 values from reef sites are correlated with oyster density (Kendall-Tau correlation coefficient, $\gamma = 0.376$, $p < 0.05$). HSI2 values from reef sites were not correlated with oyster density ($\gamma = 0.319$, $p > 0.05$). One problem encountered with the field test was that heaviest harvesting pressure occurred at mid-bay reefs with high HSI values; heavy harvesting decreased oyster density values at these reefs and weakened the correlation between HSI and oyster density. Despite differential harvesting pressure, reef sites with highest HSI values tended to have greater densities of oysters, as predicted by the model.

DISEASES OF ALASKAN KING CRABS

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In response to reports of serious declines in Alaskan king crab populations in 1982, we initiated a survey of diseases of king crabs from commercially valuable stocks in the Gulf of Alaska and Bering Sea. Through 1985, 1172 king crabs: 809 *Paralithodes camtschatica* (red king crab), 220 *P. platypus* (blue king crab), and 143 *Lithodes aequispina* (gold king crab) were necropsied, processed and examined microscopically for evidence of disease.

Serious diseases found included virus infections of the bladder and antennal gland and microsporidian infections in all three species. The prevalences relative to species infected, geographical distribution over the four-year period and the pathological effects of these and other, less important diseases will be presented.

THE TASMANIAN SHELLFISH CONTROL PROGRAM—A GROWERS PERSPECTIVE

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Tasmania, Australia, has adopted a clean waters policy for shellfish farming and implemented a program equivalent to the National Shellfish Sanitation Program. The industry is limited to hatchery produced stock as there are no naturally occurring commercial beds which reproduce regularly. This situation offers great advantages for the industry as all farms can only occur on a specific lease of sea bed and waters. Illegal activity is therefore difficult and growers risk loss of rights to the farm for contraventions of lease/license conditions. As a marketing-promotional tool the benefits are immediately obvious. Consumer confidence and product safety are factors which can be capitalized on and wider scope for marketing through exports is another plus factor. However there are costs: these may be subtle, such as provision of assistance to the monitoring staff (moral obligation) and of stock for sampling; or they may be overt, discontinuity of trading during shutdown when closure orders are enforced. This can be particularly serious in an industry heavily reliant on trading in a fresh product, "oysters natural". Competitors can thereby secure a previously occupied market place, product substitutions may occur, cash flow is seriously interrupted and, for extensive closures, product jams occur. The presentation briefly examines this alternative to artificial purification from a growers viewpoint.

RECOVERY PERIOD OF NEWLY-MOLTED SNOW CRAB, *CHIONOECETES OPILIO*, TO A HARD-SHELLED CONDITION

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During the summer of 1983 and 1984 approximately 3,500 commercial sized, soft-shelled male snow crab, *Chionoecetes opilio*, were tagged with Floy "spaghetti tags" and released onto the commercial fishing grounds. Recaptured crabs were frozen intact by commercial fishermen and held for pickup by the authors. Recovered animals were thawed in the laboratory and checked in order to determine their shell condition at time of recapture.

Recovery time varied from 2–4 months indicating that potential season closures by resource managers in order to avoid soft-shelled crabs may have to be for extended time periods in order to be effective. Size-frequency histograms, depth distributions and seasonal variations in soft-shelled incidence are discussed.

CRABS vs BAY SCALLOPS: EFFECTS OF PREDATOR AND PREY SIZE ON FEEDING RATES AND PREDATORY BEHAVIOR

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Laboratory experiments examined the size-specific interactions of 6–60 mm bay scallops, *Argopecten irradians irradians*, and nine species of crabs. Feeding rates declined as scallop size increased, or crab size decreased. Rates of predation were consistently low on individuals larger than 40 mm, but scallops achieved only a partial size refuge from crab predation because even large adults (60 mm) were sometimes attacked successfully. The sequence of predatory methods (crushing, partial crushing, chipping, prying) employed to subdue scallops of progressively larger shell size was highly consistent among different crab species. Analysis of the relative frequencies with which different scallop sizes were eaten suggested that crabs often selected prey on the basis of how easily their shells could be penetrated.

ON THE USE OF HATCHERY PRODUCED MUSSEL (*MYTILUS EDULIS* L.) SPAT IN MUSSEL AQUACULTURE

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The purpose of this ongoing study is to analyze the determinants of mortality and growth of *M. edulis* spat transplanted to the sea at about 1 mm in length in order to develop reliable methods for transplantation and early grow-out.

A method for tagging large numbers of small spat (<1.2 mm) was developed which allowed survival rates of transplanted spat to be measured. Shell pigmentation in these spat was induced by bright (11,000 lux) fluorescent light. By growing the spat under alternating 4 day periods of darkness and light, a distinctive and permanent band was depositied in the shell which allowed recognition of transplanted spat.

From direct observations and caging experiments in Tomales Bay, CA, it was found that predation by surfperch (*Cymatogaster aggregata*) was a serious concern during the summer. When present, these fish consumed 90% of transplanted spat within 10

days. However, when protected with netting, 1 mm spat could be transplanted with high survival.

The effect of initial spat density on growth and survival was also investigated. Low densities of 1–2 per cm^2 became heavily fouled. High densities of 35 per cm^2 resulted in slow growth. Intermediate densities of 5–8 per cm^2 were optimal, resulting in rapidly growing monocultures.

USING CENTRIFUGED ALGAE FOR FEEDING OYSTER LARVAE

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During 1984/5, Innovative Aquaculture Products Ltds. undertook an investigation into various aspects of centrifuging marine microalgae for use in its oyster hatchery. Of those algae species used, *Thalassiosira pseudonana* withstood the centrifuging process well and the cells were easily resuspended. *Chaetoceros calcitrans* cells were also well able to withstand centrifuging but it was necessary to use very low flowrates to acheive good recovery. *Pavlova lutheri* and *Isochrysis galbana* were prone to severe cellular damage.

When the paste of concentrated cells was stored at 4°, food value declined with time at a rate which varied considerably from one batch of algae to another: in the best case food value was still comparable to uncentrifuged cells after twelve weeks in storage, but more typically it had become significantly less within two or three weeks.

The management advantages and potential of the centrifuging technique in the context of bivalve hatcheries are outlined.

EXTENSIVE CULTURE OF PENAEID SHRIMP IN COASTAL IMPOUNDMENTS IN SOUTH CAROLINA

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Approximately fifteen percent of South Carolina's 204,300 ha of coastal marshes are impounded for waterfowl management. In recent years, these areas have become increasingly attractive for shrimp culture as an alternative to, or in conjunction with, waterfowl management.

Since 1983 several privately owned sites have been managed for extensive culture of indigenous penaeid shrimp, with yields ranging from <1 to 112.5 kg/ha. At two sites monitored during 1985, natural tidal flushing allowed extended recruitment of shrimp into impoundments and provided adequate water exchange to maintain water quality parameters within acceptable limits for survival and growth of penaeid shrimp. More extensive management (supplemental stocking, feeding, and circulation, and control of competitors and predators) may be necessary to achieve yields >100 kg/ha consistently, but such methods may be impractical in large impoundments and may not be compatible with management practices for waterfowl.

A MODEL OF THE ENERGY BUDGET OF HEALTHY AND PARASITIZED OYSTERS, WITH VALIDATION BY GROWTH EXPERIMENTS

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Energy balance is often used to describe the physiological state of marine organisms. Equations for energy budget express assimilation in terms of the costs of growth, respiration and reproduction. These calculations have rarely included energetic loss to parasites, however. In the current research, we modelled the energetic relationship between an ectoparasitic gastropod, *Boonea* (*-Odostomia*) *impressa*, and its host, *Crassostrea virginica* and then tested the outcome against laboratory results. Calculations were made for oyster assimilation and snail ingestion (assimilation/assimilation efficiency). Oyster scope for growth, or absolute growth potential, was determined by subtracting reproduction and respiration from assimilation. From parasitized oysters, snail ingestion also was subtracted from assimilation. Scope for growth then yielded a quantitative value for the potential for oysters to grow, with and without parasites. We tested the validity of our model by comparing the predicted growth of oysters (under varying parasite loads) to actual laboratory data on the growth of

parasitized oysters. The energetics model predicted that growth, for large (7 cm long) oysters, for example, with few parasites (10), would be reduced by about 25%. Large oysters with high parasite levels (30) would have a 75% reduction in energy available for growth. Small oysters (3 cm) would have a 25% reduction in growth potential at lower parasite levels (5 snails) and would have a negative energy balance at high parasite levels (15 parasites). As snail size or number increased, the reduction in scope for growth would be intensified. Laboratory experiments on growth corroborated this predicted impact of *Boonea impressa* on oysters. Field studies indicated that the number of parasites required to substantially affect oyster energy balance was commonly encountered on Texas oyster reefs.

METABOLIC RESERVES AND CALORIC CONTENT OF SIX SPECIES OF PHYTOPLANKTON CULTURED AS FOOD FOR BIVALVE LARVAE

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Phytoflagellates *Isochrysis galbana*, *Isochrysis* sp. (Tahitian variety) and *Tetraselmis suecica* and diatoms *Thalassiosira pseudonana*, *Chaetoceros calcitrans* and *Chaetoceros* sp. (A.R.C. variety) were collected at exponential and stationary phases of growth and biochemical compositions determined. Moisture content declined in all species at the stationary phase of growth. The organic content of diatoms was reduced by the high percentage of total and insoluble ash. Inclusion of lipid and protein was highest in species of *Isochrysis* with carbohydrate constituents of the phytoflagellates presenting a complex mixture of glucose, galactose, mannose, xylose, arabinose, ribose, fucose, and rhamnose. Level of carbohydrates was generally higher in diatoms than phytoflagellates with glucose the dominant sugar originating from a reserve glucan considered digestible by bivalves. Total caloric content of these metabolic reserves allowed for ranking of plankton as sources of physiological energy in the following decreasing order, *Isochrysis* sp. (Tahitian variety), *I. galbana*, *C. calcitrans*, *T. suecica*, *T. pseudonana*, and *Chaetoceros* sp. (A.R.C. variety) with all but *T. pseudonana* exhibiting higher energy levels in the stationary cells. Based on combustible energy determined by microbomb calorimetry *C. calcitrans* and *T. suecica* were exchanged in the order of ranking based on metabolic reserves.

INTERACTION BETWEEN DUNGENESS CRAB ABUNDANCE AND INFESTATION INTENSITY WITH NEMERTEAN CRAB-EGG PREDATORS

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Intensity of infestation by the crab-egg predator *Carcinonemertes errans* on populations of the Dungeness crab *Cancer magister* have varied widely at different geographic locales along the Pacific coast. The central California crab population supports massive infestations by these worms with a resultant loss of 50% or more of the eggs brooded by this population in most years. Infestation intensities of worms on crab populations in Northern California and Washington in the early 1970's were an order of magnitude lower than those of central California. Following the dramatic upturn in crab abundance in northern California, Oregon and Washington in the late 1970's nemertean densities increased in those waters to the epizootic levels typical in central California. Total worm abundance increased rapidly during the early stage of the crab resurgence but maximum nemertean density on hosts was reached 2–3 years later after crab abundance began to decline from its peak. Crab abundance declined in the early 1980's and nemertean densities have followed the crab decline but at a lag of a few years. While the 10 year data set encompasses only one cycle in the well known Dungeness crab fishery cycle, the balance between crab abundance and that of its egg-predator is reminiscent of a classic predator-prey cycle.

THE EFFECT OF THE ECTOPARASITIC SNAIL, *BOONEA IMPRESSA* ON OYSTER GROWTH AND HEALTH IN THE FIELD WITH COMMENTS ON PATCH FORMATION IN SNAIL POPULATIONS

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Field studies were conducted on the effect of the ectoparasitic snail *Boonea impressa* on oysters (*Crassostrea virginica*). Parasitized and unparasitized oysters were kept for 1 month in partially enclosed plexiglass domes in a tidal creek near Port Aransas, Texas. Growth rates in oysters parasitized with *B. impressa* were decreased significantly ($P < 0.05$) from those of unparasitized oysters. Oyster growth rate was correlated with the intensity of

parasitism; oysters with more snails grew less. Intensity of the disease-producing organism *Perkinsus marinus* was significantly higher in parasitized oysters as well. During a four week recovery period when all *B. impressa* were removed, the previously parasitized oysters grew at a higher rate than those originally unparasitized, however *Perkinsus intensity* remained above control levels. These results verify previous laboratory work showing that *B. impressa* can have an important effect on oyster health.

B. impressa are distributed contagiously in the field so that some oysters are more heavily parasitized than others. Laboratory experiments to study the formation of patches in oyster populations were conducted by arranging oysters in a circle in a flowing seawater system and placing snails in the center of the circle. Within 24 hours, snails aggregated preferentially on certain oysters. These oysters continued to recruit snails over the next few days. The experiment was repeated with the same oysters, but repositioned in the circle. Snail aggregation occurred similarly but the aggregates did not reoccur consistently on the same oyster or on oysters located in the same position as those that previously had aggregations. The level of *P. marinus* infection did not influence which oysters were parasitized. Thus, the aggregation of snails into patches on certain oysters appears to be random.

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GEOGRAPHICAL EFFECTS ON GROWTH RATE IN THE HARD CLAM *MERCENARIA MERCENARIA*

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In order to investigate the extent to which populations of *Mercenaria mercenaria* might be genetically adapted to local conditions, adult clams were collected from three geographically separated natural populations in Massachusetts, Virginia and South Carolina. These clams were divided into groups by sex and three sets of females from each location were mated with males from all three locations to produce the nine possible combinations of a factorial cross. When the offspring were ready for growout, each cross was divided into three portions and shipped to nurseries in each of the three localities. At this time, shell length was measured for a sample of 100 clams from each of the nine crosses. After six months, shell length was measured in a sample of 100 individuals from each subset of each cross.

When subjected to an analysis of variance, the data from the first samples, all bred at one location, show a strong effect of parental origin on shell length. The second set of samples, from each of the nine crosses raised in each of the three locations, continues to show a significant effect of parental origin. However, in the second samples, the location of the rearing nursery explains an even larger portion of the variation than does the geographical origin of the parental stocks. The more northerly the rearing hatchery, the larger the mean shell length achieved. Although the analysis is complicated by highly significant interaction effects, the effect of parental origin does show a clear pattern. While each cross performed better in more northern waters, within any one nursery those clams with higher proportions of southerly parental contribution tended to grow larger. This is interpreted to mean that stocks from southern areas are able to take greater advantage of preferred growing conditions.

GROWTH AND SURVIVAL OF *CRASSOSTREA RHIZOPHORAE* OF DIFFERENT SPAT SIZE UNDER SUBTIDAL CULTURE CONDITIONS

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The mangrove oyster, *Crassostrea rhizophorae* is currently being cultivated on a pilot commercial scale in the Caribbean Island of Jamaica. This oyster has also been considered as a candidate species for coastal pond culture in at least one temperate region (France). Under certain culture conditions, this oyster has fast growth rates, excellent shape, taste and quality.

The practice of culling the early slow-growing oyster spat in both intensive and extensive culture systems is aimed at growing-out oysters of relatively uniform sizes and taking the shortest time to obtaining marketable size. In field experiments between August–December 1986, oysters of comparable age which were collected intertidally, were divided into different size classes and grown subtidally. Initial size relationships to final survival and size are presented. Growth and survival of these oysters seem more related to the impact of competitive and predatory biological agents than to genetically influenced traits.

INDUCED TRIPLOIDY IMPROVES THE PHYSIOLOGY, NOT THE GENETICS, OF CULTURED SHELLFISH

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Induced triploidy is a useful procedure to improve the physiology of cultured shellfish, when reproductive effort interferes with desired production characteristics. For example, triploid Pacific oysters (*Crassostrea gigas*) exhibit profoundly altered reproductive physiology as evidenced by type and degree of gametogenesis, growth during the reproductive period, nutrient storage and utilization, and physiological energetics. However, these changes are not genetic so much as genetically mediated alterations in physiology because of reproductive sterility. Induced triploidy is therefore more akin to the benefits derived from improved culture conditions than it is related to genetic improvement. Theoretically, triploids can be produced for any species in selected or wild stocks in order to improve performance. Like any tool, triploidy is suitable in some situations, and not in others. Suitable situations are those in which reproductive effort substantially reduces or interferes with desired production characteristics of cultured bivalves. Where reproductive effort does not interfere, triploids are more or less useless.

Factors to be considered for evaluating induced triploidy in culture programs include species fecundity, seed sources, triploid verification, market criteria, and of course projected economic benefits.

THE EFFECT OF SESTON ON THE GROWTH OF BIVALVES AT THREE DEPTHS IN LONG ISLAND SOUND

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Short term and long term experiments were conducted to determine if seston has a positive effect on the growth of suspension-feeding bivalves. Two species were used, *Crassostrea virginica*, the American oyster, and *Mytilus edulis*, the blue mussel.

The short term experiment consisted of monthly growth trials, comparing growth during stratified and destratified conditions. Mussels and oysters were deployed at three positions in the water column; above, below and at the approximate depth of the thermocline. During stratification, when chlorophyll concentrations were highest at the surface, growth was greatest at the surface and decreased with depth. After destratification, growth at the bottom was the same or less than at the surface.

The long term experiment was conducted over four months. Oysters were deployed near the surface and near the bottom under stratified conditions. After destratification the positions were reversed, with those near the surface moved to the bottom, and those near the bottom moved to the surface. Controls were also maintained continuously near the surface and near the bottom. Those grown continuously near the surface had the best tissue growth. After destratification, when chlorophyll concentrations did not change with depth, increasing seston had no positive effect on growth.

In past studies, researchers found that bivalve growth could be enhanced by the presence of seston in the diet. It was postulated that inorganic particles improved digestion, or that organics associated with seston complemented the algal food supply. However, in Long Island Sound, bivalve growth appeared to be influenced primarily by chlorophyll distribution.

MANAGING A PREDATOR: DECLINE OF AN OFFSHORE BUSYCON FISHERY

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The commercial whelk fishery in South Carolina started in the spring of 1978 when shrimp fishermen began harvesting knobbed and channeled whelks following a poor shrimp season. Larger mesh nets were adapted to trawl for whelks offshore of the State's barrier islands. Whelk trawlers increased from two in 1978 to 45 in 1984. Declining catch per unit effort within populations and increasing numbers of whelks per bushel indicate a declining fishery and limited recruitment. Mark and recapture results reinforce the likelihood of a reduced resource for a number of years. As a result, the alternative fishery has become less attractive and concurrently self-regulating.

OBSERVATIONS ON THE INCIDENCE AND OCCURRENCE OF HERMAPHRODITISM IN THE SOFT-SHELL CLAM, *MYA ARENARIA*

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Mya arenaria is a gonochoristic species; only rare cases of hermaphroditism have been reported. New observations were obtained from clams sampled during a broad field survey and from clams sampled for use in experiments.

In the field survey 34 sites were sampled ranging from Chesapeake Bay to Nova Scotia. Over 5,700 individuals were examined histologically. Only 4 hermaphrodites were found (0.07% total incidence): 1 from New Bedford, Mass. (0.55% incidence) and 3 from Chesapeake Bay (0.86% incidence). These results are similar to previous observations indicating a significantly higher incidence in Chesapeake Bay compared to more northern areas. Relative to other northern sites, finding a single hermaphrodite at New Bedford was not considered significant and may be due just to random chance.

Two samples (864 clams each) were taken from Chesapeake Bay to Rhode Island for use in bioassay experiments, where they were sampled 3 times at 2-month intervals starting in August. Both samples showed a high incidence of hermaphroditism (2.78%, 0.93%), thus confirming the field observations. The large number of hermaphrodites found allowed further characterizations to be made. Both bilateral and mixed-follicle hermaphrodites were found; the former condition was dominant, occurring in a ratio of 2.75:1. In addition, several individuals had both bilateral and mixed follicles, a condition previously unreported. Representative individuals were found for each stage of gonadal development. No consistent differences were observed between the relative stages of development of spermatogenesis and ovogenesis.

DISTRIBUTION, ABUNDANCE AND HABITAT ASSOCIATIONS OF DUNGENESS CRAB, *CANCER MAGISTER*, IN GUEMES CHANNEL, SAN JUAN ISLANDS, WASHINGTON

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Dungeness crab populations at the site of a proposed marina development near Anacortes (north Fidalgo Island), Washington were studied from August 1984 through April 1986. Crabs were sampled seasonally using a small beam trawl, commercial crab pots modified to retain small crabs, SCUBA diver transects and by the collection of 0.25 m^2 quadrat samples dug at low tides.

Young-of-the-year (0+) crabs recruited to the benthos from June through September and their density was greatest in intertidal areas of eelgrass (*Zostera marina*) and algae (especially *Ulva*). The nearshore subtidal populations were dominated by 1 to 3-year old crabs which utilized both eelgrass habitats and open, sandy areas.

An important finding of this study was that ovigerous females selectively aggregated in a very shallow depth band (1 to 3 m below MLLW) highly associated with the eelgrass beds. This aggregation occurred primarily along the north shore of Fidalgo Island and consisted of about 60,000 ovigerous females. These females remained buried in the bottom sediments for extended periods of time and could only be sampled by SCUBA divers. The proposed marina development was subsequently redesigned to avoid impacts to this important ovigerous female habitat.

POPULATION DISTRIBUTION OF HARD CLAMS IN THE INDIAN RIVER LAGOON, FLORIDA

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Hard clams (*Mercenaria* spp.) were sampled in the Indian River Lagoon, Florida, during the summer of 1986. Clams were abundant throughout the central region of the sampling area, but were scarce on both the northern and southern extremes. Patterns of environmental variability are invoked to explain the macro-distribution of the animal in the lagoon, whereas water depth and sediment composition influence small-scale distribution patterns. A study of internal growth lines is utilized to explain the recent history of hard clams in the lagoon. Information on the age distribution of the population elucidates the pattern of annual recruitment in the population. This is considered in light of macro-scale disturbances which impact on the lagoon.

PREDATOR-HARD CLAM (*MERCENARIA MERCENARIA*) INTERACTIONS: SPATIAL SCALE EFFECTS

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Predation studies have generally focused on the effects of density of the prey organism. While prey density is an important nearfield parameter regarding predator induced mortality, other parameters such as prey patch size, predator density, and predator distribution also influence mortality rates. Direct underwater observations of the foraging activities of crustacean predators revealed these types of parameters to be important.

A manipulative field experiment was conducted to determine the covarying effects of juvenile clam patch size and density on survivorship ($\bar{x}$ SL = 3.45 mm, S.D. = 0.38 mm). A complete 3 × 4 factorial design was used with 3 densities (25, 150, and 300 clams/.25 m^2). Patch size had a very significant effect ($p < 0.005$) on survivorship; the larger the patch, the greater the mortality. The density effect was only slightly significant ($p < 0.10$). The interaction of both variables was not significant.

Clams exhibit an escape response due to the foraging activities of predators. A laboratory experiment demonstrated a significant decrease in growth of juvenile hard clams ($\bar{x}$ SL = 1.2 mm, S.D. = 0.275; at start) subjected to foraging by hermit crabs (*Pagurus longicarpus;* 12.8/.25 m^2) when compared to a treatment with no predators (t-test, $p = 0.05$). This effect caused individuals to grow at a slower rate and be available longer to a more diverse predatory milieu. Future experiments will examine the role of varying predator densities in the interaction.

The shelter related behavior of some crustacean species restricts the area searched during part of each 24 hour period. The densities of shelter sites and predators, and apparent diel patterning of search area by predators may affect the spatial mortality patterns of prey species. An experimental approach to this problem will elucidate predator distributional effects on prey mortality.

FUNCTIONAL ANATOMY OF *PLACOPECTEN MAGELLANICUS* GILL AND IMPLICATIONS FOR NUTRITION

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The organisation, general anatomy, and micro-anatomy of the *Placopecten magellanicus* gill were studied using histology, stereomicroscopy, scanning and transmission electron microscopy. In addition to correcting earlier presentations of this structure, several new observations are reported.

Micrographs showing the structure of the dorsal respiratory expansion are presented for the first time. The cellular anatomy of the interconnecting vessels indicates particularly active transport of diffusion in this region.

The entire abfrontal surface of the principal filament, including the dorsal respiratory expansion, is densely ciliated and mucosecretory. These characters may aid in the establishment of a respiratory current and in the prevention of gill damage during escape responses.

All ciliated cells present a vesicular matrix which covers the ciliary bases at the apical surface. This matrix may effect some mechanical function for which mucus could be unsuitable.

All nonciliated regions of the gill filaments are observed to be covered with microvilli, thus greatly increasing the surface area of the gill. Stereo-microscopic observations of living animals shows that symbiotic ciliate protozoans are constantly dislodged from the gill filaments and transported via a mucus string to the buccal region. The nutritional implications of these observations are discussed.

THE EFFECT OF EPIBIONTS ON THE GROWTH OF *MYTILUS EDULIS* CULTURED IN LONG ISLAND SOUND

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This study was designed to test the feasibility of culturing mussels to a commercial size in one growing season. Yearling mussels, collected from nearby mussel beds, were placed in net tube sacs and suspended from rafts located at Stony Brook Harbor, Smithtown and Flax Pond, Old Field, New York. The growth rates and yields of the mussels were examined. On one half of the lines on each raft, all of the fouling organisms which were relatively easy to detach were removed. The rest remained uncleaned.

With the use of yearling seed, a crop of market-size mussels was produced in one season (May–December). At the time of harvest, all parameters measured (condition index, shell length and volume, ash free dry weight, and amount of fouling per shell length) were significantly greater for the mussels cultured at Stony Brook Harbor than for those from Flax Pond.

Furthermore, there was no significant difference between mussels that were cleaned and those that were left uncleaned during the culture period for any of the parameters measured.

Following the methods of Theisen (1972), laboratory experiments were performed to examine the effects of temperature, size, and condition of the shell on the cleaning behavior of mussels. Experiments utilized several sizes of mussels with varying shell condition for several naturally occurring temperature regimes. The frequency of shell cleaning behavior exhibited was found to be significantly lower ($p = .05$) for decreased temperatures (-1 to 10°C) than for warmer temperatures (16–20°C). This suggests that cleaning is reduced in the winter months during the period of peak barnacle settlement. This reduction in cleaning may explain the heavier set of barnacles relative to other fouling organisms found on mussels.

PREDATION OF MUD CRABS AND BLUE CRABS BY TOADFISH *OPSANUS TAU*, WITH A DISCUSSION OF BIOLOGICAL CONTROL OF CRABS IN MOLLUSCAN AQUACULTURE

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Mud crabs (Family Xanthidae) of four size classes (8.0, 18.5, 28.0 and 37.5 mm mean carapace width [CW] were offered to five size classes of toadfish *Opsanus tau* (84.3, 128.4, 178.0, 225.6 and 283.0 mm mean total length [TL]) for 48-hr. Predation rate, recorded as the number of dead crabs · fish-1 · day-1, was directly proportional to toadfish size and inversely proportional to crab size. Toadfish of 283.0 mm TL had predation rates of 3 crabs · fish-1 · day-1 on mud crabs of 28.0 mm CW. Toadfish could cause significant mortalities on mud crabs one tenth their size (CW/TL).

Blue crabs *Callinectes sapidus* of 77.8 to 105.3 mm CW were exposed to toadfish of 196 to 322 mm TL in the presence of juvenile hard clams *Mercenaria mercenaria* of 4.3 to 6.5 mm shell height with sand, gravel or hard bottom substrate for 24 to 96 hrs in the laboratory. Toadfish could injure or kill blue crabs of almost one third their size. Crab predation on clams was reduced with the presence of toadfish or gravel. The use of toadfish as a biological control of crab predation in molluscan aquaculture is discussed.

THE EFFECT OF AIR-SUPERSATURATED SEA-WATER ON *ARGOPECTEN IRRADIANS* (LAMARCK) AND *CRASSOSTREA VIRGINICA* (GMELIN) WITH REFERENCE TO GAS BUBBLE TRAUMA

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Argopecten irradians and *Crassostrea virginica* were exposed to several different levels of supersaturated seawater at temperatures ranging from 10 to 21°C. Gas bubble trauma occurred at a total gas saturation level of 116%, causing mortality in juvenile *A. irradians* and reduced growth in juvenile *C. virginica*. A review of the effect of air-supersaturated seawater on bivalves is presented with a discussion of the difference in tolerance levels.

OPTIMIZING COLLECTION OF PECTINID SPAT ON COLLECTORS

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Collecting spat on artificial collectors is the first step for culturing scallops in the natural environment. The spat settlement period was determined at Gascons, Baie des Chaleurs, Quebec, in 1986. During the autumn months, series of collectors were placed in the water every 2 weeks for immersion periods of 2, 4, and 8 weeks. Peak settlement occurred between October 28 and November 11. The immersion period and the depth of collectors are two important factors that affect settlement intensity. For collectors immersed 4 and 8 weeks, settlement intensity was several times greater than for collectors immersed 2 weeks prior to settlement. Settlement intensity along a depth gradient in 25.5 meters showed greatest numbers between 9 and 22.5 meters with relatively low numbers near the surface and the bottom.

SCALLOP RESOURCES OF BRITISH COLUMBIA, CANADA

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Thirteen species of scallops have been recorded from British Columbia waters but most are small or rare. Four species, weathervane, *Patinopecten caurinus*, rock, *Crassadoma gigantea*, pink, *Chlamys rubida*, and spiny, *C. hastata*, are either large or occur in sufficient abundance to elicit enquiries about potential commercial fisheries. Populations of weathervane and rock scallops are too sparse to support commercial fisheries but a small dive and dragging fishery exits for pink and spiny scallops but annual landings are under 50 t whole weight. Results of studies on these four species over the past twenty years are presented. The conclusion of this work is that populations of the four species are too small to support a significant sustained fishery, annual landings of 500 t or more. If a large scallop industry is to develop in British Columbia it will have to rely on culture or enhancement technology.

PROTOZOAN PARASITES OF PACIFIC OYSTERS (*CRASSOSTREA GIGAS*) IN BRITISH COLUMBIA

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In addition to the abundant protozoa (mainly ciliates) found around the gills and in the mantle fluid of Pacific oysters from 15 localities in British Columbia, four species of parasitic protozoa were observed in association with tissues. An unidentified species of *Trichodina*, usually attached to the mantle, was observed in oysters from all but one locality with a prevalence of 23% to 100% per locality and mean intensity of 11 ciliates per infected oyster. Even in the heaviest infection (about 312 *Trichodina* in one oyster), there was no evidence of associated pathology. Another ciliate that produced no evidence of pathology, was identical in morphology to *Orchitophrya stellarum*, and was found within the digestive gland tubules of 7% to 37% of the oysters from all localities. The majority of the infections were light (from 1 to 9 specimens per wet mount preparation of digestive gland tissue) and only 2.6% of the infected oysters had more than 25 *Orchitophrya* per preparation. A microcell, the causative agent of Denman Island disease, was observed only in oysters from one beach on Denman Island. Unlike *Bonamia ostrea*, the microcell in *C. gigas* was localized within the green focal abscesses and intracellularly in vesicular connective tissue immediately surrounding the lesions. About 30% of the older age oysters on the low part of the beach are affected in the spring of each year and although many apparently succumb to the infection, some survive and the lesions heal. Another protozoan, that is possibly pathogenic to

young oysters, but does not produce gross lesions, is a gregarine of unknown specific identity and life cycle. The parasite was observed histologically in the connective tissues of oysters from only 2 localities and is most prevalent (35% infected) in oysters from Pendrell Sound.

A CASE STUDY OF HISTOPATHOLOGY IN *MACOMA CARLOTTENSIS* (BIVALVIA, TELLINIDAE) RELATED TO MINE-TAILINGS DISCHARGE AND REVIEW OF POLLUTION-INDUCED INVERTEBRATE PATHOLOGY SHADES OF SELYE?

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The prevalence and severity of histopathologies in an example mollusc, *Macoma carlottensis*, Whiteaves, 1880 were qualitatively examined in Howe Sound, British Columbia. Copper-mine tailings were deposited into Howe Sound from 1899 to 1974. Histopathologies of the digestive diverticula, ctenidia, and ventral foot epithelium appeared to be related to distance of the clam from the original point-source tailings discharge. Other tissues affected less severely were gastrointestinal epithelia, kidney, and possibly ovary.

Several histological changes were similar to those described for other stressors and species; for example, swelling of gill filaments followed by loss of ciliated frontal cells, uncoupling of interfilamentar junctions, vacuolation of gill epithelial cells, and in extreme cases necrosis. In the digestive diverticula, non-specific histopathologies include desquamation or increased fragmentation of digestive cells, vacuolation, lysosomal destabilization, and haemocyte invasion.

Emerging patterns of physiological and cytochemical responses to a wide variety of stressors may reflect a General Adaptation Syndrome in invertebrates paralleling Selye's G.A.S. in humans. Extension of the G.A.S. may aid in the understanding of shellfish response to natural and anthropogenic stress.

GROWTH AND SURVIVAL OF LARVAL AND JUVENILE POLYPLOID CLAMS, *MERCENARIA MERCENARIA*

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Five families of *Mercenaria mercenaria* were produced by spawning adults of known genotypes. Following fertilization, ploidy-altering treatments of one mg/L cytochalasin B in 0.1 percent dimethylsulfoxide were applied at two times. Both DMSO controls and nontreatment controls were run. Resulting larvae were reared in static culture at a density of less than 5/ml and fed monocultures of Tahitian *Isochrysis*. Cultures were sampled at critical stages to determine survival. Growth was monitored in post-set and juvenile populations. When populations reached a minimum size of 2–3 mm, ploidy was determined utilizing an Ortho Spectrum III flow cytometer. Polar body production was analyzed in three different families at three different temperatures. Samples were taken at five minute intervals beginning immediately after fertilization. Samples were stained with Hoescht stain and analyzed under a fluorescent microscope. Polar body production, growth, survival and ploidy alteration were analyzed with respect to treatments and families.

EFFECTS OF FLOW VELOCITY, FOOD CONCENTRATION, AND PARTICLE FLUX ON GROWTH OF JUVENILE BAY SCALLOPS, *ARGOPECTEN IRRADIANS*

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Growth rates of suspension feeding organisms are determined by many interacting factors, efficiency of particle capture and food particle concentration being two of the more influential. Flow regimes affect both the efficiency of particle capture and the number of particles available to the animal per unit of time. Flume studies were conducted to examine the growth rates of juvenile bay scallops *Argopecten irradians* in three flow velocities (1.6, & 15 cm/sec) over a range of food concentrations (6000–80000 cells/ml). The three channels of the experimental flume, each running at a different flow rate, were gravity fed from a single reservoir. Juvenile scallops (3–10 mm) were positioned on rigid eelgrass mimics, and placed in the flume channels. The flume was stocked with the proper concentration of algae (Tahitian *Isochrysis* sp.) and flows were gradually increased to experimental levels.

Particle flux (algal cells/cm²/sec) passing by the scallops is the product of food concentration (cells/ml) and flow velocity (cm/sec). Initial results show differences in growth (shell dimensions, but not weight) within a given flux of food particles. These differences were due to interactions between flow velocity and food concentration, not due to differential food fluxes. This result suggests that measurement of flux alone is a poor predictor of growth. Preliminary results also showed food concentration to be more important than flow velocity. It is possible that elevated food concentrations compensate for stressful flow velocities. Further experiments are underway to test this hypothesis.

ASSESSING THE CARRYING CAPACITY OF A MUSSEL CULTURE OPERATION: A PRELIMINARY STUDY

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Water exchange, food levels and mussel filtration rates were monitored from May to October 1986 at a mussel culture operation on the eastern shore of Nova Scotia. The water exchange in the inlet varied from 14 to 31% per tidal cycle, or 28 to 48% of the basin volume renewed per day. Particulate organic matter (POM) decreased from 1.1 to 0.3 mg/l from May to October, whereas chlorophyll *a* levels increased from a minimum of 0.6 µg/l in May to 3.1 µg/l in September. Mussel filtration rates, determined in grazing chambers at the site, ranged from 1.2 to 2.5 l/h for market-sized mussels (50–60 mm). From these data we calculated the approximate carrying capacity of the inlet for mussel culture. This estimate is compared to values derived from other carrying capacity models.

COMPARATIVE TOXICITY OF CULTURED ISOLATES AND NATURAL POPULATIONS OF *PROTOGONYAULAX TAMARENSIS* (LEBOUR) TAYLOR FROM THE ST. LAWRENCE ESTUARY

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The occurrence of paralytic shellfish poisons in shellfish from the lower St. Lawrence estuary has been associated with the presence of the toxic marine dinoflagellate *Protogonyaulax tamarensis* (Lebour) Taylor. Net samples of mixed phytoplankton assemblages within which *P. tamarensis* was dominant were collected from stations on both the north (Baie-Comeau region) and south (Rimouski region) coast of the lower estuary. The toxin levels of these natural assemblages were compared with those of unialgal cultured isolates from the region, by means of the conventional mouse bioassay. Acid-hydrolysed extracts were also assayed using a toxin analyzer, which yielded total toxicity values based upon fluorescent oxidation products.

In general, toxin levels from natural assemblages were substantially higher than those from cultured isolates grown under standard conditions. However, there was considerable unattributable variation in toxicity for both groups. On a per cell basis, toxin content of the natural populations was among the highest ever reported for *Protogonyaulax*. This suggests that under favourable conditions for bloom formation, shellfish in the St. Lawrence region may become rapidly and dangerously toxified by even moderate concentrations of these dinoflagellates in the water column.

DISTRIBUTION OF TOXIC CYSTS OF *PROTOGONYAULAX TAMARENSIS* (LEBOUR) TAYLOR IN NEARSHORE SEDIMENTS FROM THE NORTH COAST OF THE ST. LAWRENCE ESTUARY

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The quantitative distribution of toxic cysts of *Protogonyaulax tamarensis* (Lebour) Taylor was investigated along the northern shore of the St. Lawrence estuary. Nearshore sediments sampled during the summer, prior to the development of significant concentrations of motile *Protogonyaulax* cells in the water column,

revealed only low cyst concentrations. However, in autumn, several weeks after the disappearance of *Protogonyaulax* from the water column, cyst concentrations at the same stations were markedly elevated. Although the distributional pattern was rather variable, certain general trends were noted. First, higher cyst numbers were associated with fine-grained sediments, as opposed to more granular substrate. Second, the highest cyst concentrations were found just adjacent to, rather than within, the core region most strongly influenced by the freshwater plume of the Manicouagan Aux-Outardes river outflow. Finally, stations with the highest cyst concentrations corresponded to areas characterized by the highest historical levels of paralytic shellfish toxicity. The evidence suggests that cyst distributions and consequent blooms in the St. Lawrence estuary are highly dynamic and strongly controlled by hydrodynamic factors. The hypothesis that the toxic blooms which appear on the south shore may originate through exogenous transport from the northern shore is further supported.

SEASONAL LYSOZYME ACTIVITY IN THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*

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It has been suggested that lysosomal enzymes (e.g. Lysozyme) may play a significant role in the defense of bivalve molluscs against invading parsites. Lysozyme activity was found in both the serum an hemocytes of the hemolymph of *Crassostrea virginica*. Lysozyme is able to lyse several species of bacteria (e.g. *Micrococcus lysodeikticus* and *Bacillus subtilis*, etc.). The two pathogens, *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX) are the primary cause of oyster death in Virginia waters, especially in mesohaline areas during warm seasons. An earlier study on lysozyme activity in pooled sera from hemolymph of oysters indicated seasonal variations in lysozyme activities and that parasitic infection may affect it. Studies are now underway to determine whether lysozyme activity in oysters is associated with seasonal changes in water temperature and salinity, with the nutritional status of the oyster or with infection of the disease *P. marinus*.

In this study lysozyme activity in individual oysters was measured. Preliminary results reveal that there are large variations in lysozyme activity among individual oysters. It also appears that lysozyme activity in oysters is related to water temperature rather than to the level of *P. marinus* infection, although, in general, oysters infected with *P. marinus* have lower lysozyme activity. Lysozyme activity in oysters is higher when the seasonal water temperature is lower. Variability in sera protein content among individual oysters was high, but protein levels of the oyster were not correlated with the lysozyme activity. Protein levels were found depressed in *P. marinus* infected oysters.

QUANTITATIVE GENETIC SELECTION IN THE FUTURE OF SHELLFISH CULTURE

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Genetic selection for quantitative (polygenic) traits has been the most important tool in the improvement of agriculturally important animals and plants, and there is limited evidence suggesting that the practice would be effective in the improvement of shellfish traits. A handfull of papers cited by Newkirk (Aquaculture 19:209, 1980) and a few more recently suggest that additive genetic variance that could lead to successful selection programs exists in oysters (*C. gigas*, *C. virginica*, and *O. edulis*) and in the blue mussel (*M. edulis*). This conclusion is supported by successful selection for disease resistance in the oysters (*C. virginica* and *C. gigas*) summarized by Haskin and Ford (EIFAC/FAO Symposium, Bordeaux, France. May, 1986) and for growth rate in the hard clam (*M. mercenaria*) by the preliminary studies of Chanley (*Proc. Natl. Shellfish. Assoc.* 50:163, 1961) and the continuing multigeneration studies of Castagna (unpublished).

In order to produce useful results for the shellfish breeder multigeneration selection efforts that require long-term commitment are necessary. It seems likely that useful results must emerge from grant supported research before shellfishery interests will be stimulated to initiate quantitative genetic selection efforts themselves. Clearly successful selection for increased growth rate could be profitable as could selection for increased proportion of edible parts and, as needed, for disease resistance. Traits relating to taste should be responsive to selection, but little successful effort has been conducted with farm animals perhaps because the trait is too subjective.

SPAT SETTLEMENT AND EARLY GROWTH OF *PLACOPECTEN MAGELLANICUS* IN PASSAMAQUODDY BAY, CANADA

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Adult *Placopecten magellanicus* spawn between July and September in Passamaquoddy Bay, and larvae are present in the water column from July to October. Observations on spat settlement in collectors, however, indicate the major settlement takes place during a period of about 2 weeks; and this time of settlement varies from year to year, occurring from late August to October. Numbers of spat per collecting bag were relatively constant from year to year $\overline{X}$-200–400) but varied with depth. After settlement in September, spat reach a mean height of 5 millimeters (mm) by December and 40 mm by the next November in suspended culture. Natural bottom growth is slower. Depending on site, mean height ranges from 25–35 mm after the first summer of growth.

THE REPRODUCTION CYCLE OF THE GIANT SCALLOP *PLACOPECTEN MAGELLANICUS* IN THE SOUTHERN GULF OF ST. LAWRENCE AND PASSAMAQUODDY BAY

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In 1984 and 1985 gonads from *Placopecten magellancius* were collected from Baie de Chaleur and northern, central, and southern areas of the Northumberland Strait. In 1985 and 1986, gonads were collected from Passamquoddy Bay.

The temporal evolution of the gonad maturation in *P. magellanicus* was determined from histological preparation of gonad sections. Geographical and temporal variations were observed in the timing of the maturation cycle. Results are presented, and histological changes along the reproductive cycle are discussed.

PATTERNS OF OVA ENCAPSULATION IN *BUSYCON CARICA*: ALLOMETRIC AND ENERGETIC RELATIONSHIPS BETWEEN ADULT SIZE AND REPRODUCTIVE OUTPUT

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The energetics of reproduction in the whelk, *Busycon carica*, was examined in southern Massachusetts. Egg laying behavior, and variation in clutch size, developmental period and the relative investment of energy in embryos and capsules with respect to female size are described for a small population of whelks in Cape Cod waters. Loose aggregations of female whelks deposit spawn masses subtidally in August and early September. Developmental periods ranged from 12–33 weeks; the length of the developmental period being dependent on the timing of initial deposition. Egg capsule size and volume are related to female size in *Busycon* with embryo density per capsule, clutch size and the total caloric investment in embryos and capsules increasing with adult size. In this whelk, over 50% of the energy invested in reproductive structures is allocated to capsule construction.

In addition, variation in the pattern of ova packaging among capsules within the same spawn mass is described. The size of emerging snails is highly correlated with initial ova density, and suggests that differential hatching size is a function of the initial allocation of intracapsular fluid, or albumen. These results are discussed with respect to probable extra embryonic nutrition during development in *Busycon*.

SUBSTRATE TYPE AND PREDATORY RISK: EFFECTS ON MUD CRAB INTERACTION WITH JUVENILE HARD CLAMS

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Xanthid mud crabs, such as *Neopanope sayi*, are significant predators of juvenile hard clams, *Mercenaria mercenaria*, in Long Island waters. Abundance and survival of both mud crabs and hard clams are affected by substrate type and predatory risk. In binary substrate-choice experiments, mud crabs preferred broken oyster shell most, followed in order by large gravel (>30 mm diam.), small gravel (<17 mm diam.), mud, and sand. Mud crab preference for substrates such as gravel or broken oyster shell may result in decreased susceptibility to predation. When substrate combinations contained juvenile hard clams (250 8.8–11.0 mm clams per substrate; 1000 clams/m^2), crab predation was lower in sand than in small gravel (82.2% less), large gravel (68.1% less) or small gravel overlaid with sand (64.8% less).

Crab behavior and activity patterns in these substrate combinations were determined from video time-lapse recordings and visual observation. Addition of a predator on mud crabs, the toadfish, *Opsanus tau*, caused a reduction in crab-induced mortality of clams in individual substrate trials (97.6% less in sand, 91.3% less in small gravel). This effect is primarily a result of depressed crab activity, rather than direct crab mortality. In areas where mud crab predation is of primary concern to mariculturists, clam survival may be increased by planting in sand substrates, for which crabs have a low preference. Additionally, mud crabs may be more vulnerable to their natural predators in such substrates.

"BROWN TIDE" ALGAL BLOOMS SHADE OUT EELGRASS

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Widespread decimation of eelgrass (*Zostera marina*) meadows occurred as a result of the 1985–1986 "brown tide" algal blooms in Long Island embayments. The dense blooms of *Aureococcus anorexefferens* dramatically reduced light penetration into the water column. As a consequence, biomass and the maximum depth penetration of eelgrass were reduced. The reduction in maximum depth penetration translated into 112 km^2 of bay bottom that could not support eelgrass growth as a result of the algal blooms. Eelgrass meadows serve as a nursery and habitat for many shellfish species, including the bay scallop (*Argopecten irridans*) and hard clam (*Mercenaria mercenaria*). Previous studies have demonstrated the importance of eelgrass in providing optimal hydrodynamic regimes for bay scallop and hard clam feeding, along with providing protection from predators. Recolonization rates of eelgrass are relatively slow (years to decades), even without a reoccurrence of the blooms. Consequently, the impact of the blooms on shellfish in Long Island waters will last well beyond the impact observed during the blooms. Possible reoccurrence of the blooms and slow rates of eelgrass recolonization may promote a shift from a benthic dominated ecosystem to a pelagic dominated ecosystem.

COMMERCIAL FISHERIES ANALYSIS OF *BUSYCON* WHELKS IN VIRGINIA

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Dockside sampling of four commercial fisheries was conducted from June 1983 through August 1984 to determine whelk catch composition (n = 1260). The knobbed whelk, *B. carica*, contributed 73 percent of total whelk landings, comprising nearly 100 percent of the whelk dredge fishery and otter trawl fishery whelk bycatch. The channeled whelk, *B. canaliculatum*, contributed 15 percent of whelk landings. Nearly 100 percent of the crab pot and 25 percent of the surf clam fishery whelk bycatch consisted of the channeled whelk. The lightning whelk, *B. contrarium*, contributed 13 percent of total Virginia whelk landings, occurring only in the surf clam fishery and contributing 75 percent of the bycatch.

Monthly shell lengths and widths and total, body and foot weights varied significantly for the knobbed and channeled whelk, but not for the lightning whelk. Females had significantly greater size and sex frequencies than males for all species. Estimated meat yield averaged 15 percent of total weight, or 30 percent of total body weight for all species.

Analysis of commercial landings by species and gear from 1940–85 was performed from dockside sampling and historical whelk landings. Peak whelk landings of over 1 million lbs occurred in 1974 and 1975. Landings in 1986 totaled 550,000 lbs. Dockside value rose from a low of $0.14/lb in 1976 to $0.60/lb, or about $12/bushel, in 1986.

HETEROZYGOSITY, GROWTH, AND LINKAGE DISEQUILIBRIUM IN HYBRID POPULATIONS OF *MERCENARIA MERCENARIA*

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Lines of the hard clam, *M. mercenaria*, have been selected for fast growth by Aquaculture Research Corporation and Virginia Institute of Marine Science. These lines do not seem to be inbred, judging from allele frequencies at seven enzyme loci, although there is evidence of genetic drift and loss of rare alleles. Very little relationship between heterozygosity and growth was detected in the offspring of individual crosses between these two lines, nor does variance at any particular enzyme locus seem to affect growth. We do, however, report evidence of loose linkage disequilibrium between alleles at a variety of enzyme loci and alleles at loci affecting growth in the nursery.

CHARACTERISTICS OF A FEMALE DUNGENESS CRAB, *CANCER MAGISTER*, AGGREGATION IN PORT GARDNER, POSSESSION SOUND, WASHINGTON

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Dungeness crab were sampled in Port Gardner, Washington at 2 to 3-month intervals during 1986 using a small beam trawl. Trawling was conducted at up to 63 stations at depths from 10 m to 165 m. Additional sampling was conducted during the winter using SCUBA diver transects and the Canadian Research Submersible *PISCES IV* to define the distribution of the ovigerous females which were difficult to sample due to their burial behavior.

The results of the trawl survey showed that the deeper areas of Port Gardner provided important habitat for mature crabs at average estimated densities of about 100 crabs/hectare. Females comprised about 90% of the total catch and favored depths from 20 to 100 m, especially along the "nearshore slope." Males were relatively rare and generally preferred the shallower depths (10–20 m). The distribution of females changed by season. Females were found primarily along the nearshore slope (20–80 m) during late winter to early summer. The females dispersed somewhat from mid-summer to early fall, occurring at low densities in the deeper portions of the bay (down to 140 m). During the winter, the ovigerous females aggregated in the shallower areas of the nearshore slope and occupied a distinct depth band from about 10 to 40 m depth, a distribution confirmed by SCUBA divers and the *PISCES IV*.

TRIPLOID AND DIPLOID HYBRIDS BETWEEN THE OYSTERS *CRASSOSTREA GIGAS* AND *C. RIVULARIS*: PRODUCTION, DETECTION AND POTENTIAL

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A complete factorial design was used to produce monospecific and interspecific, diploid and triploid oysters. To produce triploids, newly fertilized eggs were treated with cytochalasin B from 30–45 min after fertilization at 25°C. One replicate was spawned in June and another in September 1986. Although a disparity in broodstock condition between the replicates prevented averaging their results, it helped separate maternal and paternal influences on survival to straight hinge and triploid induction.

Survival from fertilization to 48 hours reflects the extent of incompatibility between the species and the negative effects of cytochalasin B. All monospecific crosses outsurvived their interspecific equivalents. Furthermore, diploid crosses outsurvived their triploid counterparts. The maternal influence was greater than the paternal on survival with one exception: diploid *C. rivularis* female X *C. gigas* male survived ten times better than its reciprocal in both spawns. After 48 hours survival rates were comparable and some larvae set in all 8 crosses. These are the first reported interspecific molluscan triploids.

The importance of sperm quality on induction success is shown by comparing the results for the monospecific triploid crosses. In June, when the two species were comparably mature, both yielded around 50% triploidy. While in September, when *C. gigas* was resorbing, its percentage dropped to 7%. Similar results were found with the interspecific triploid crosses. Ripe sperm ensures rapid fertilization to yield synchronously developing eggs which are needed to treat effectively with cytochalasin B.

Triploid proportions were determined using a flow cytometer. Flow cytometry also confirmed true hybridization which could not be determined either karyologically or morphometrically.

The aquaculture potential of different crosses will be discussed.

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LATITUDINAL CLINES IN SHELL MORPHOLOGIES OF *BUSYCON CARICA*

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Specimens of *Busycon carica* (Gmelin, 1791) were collected from five latitudinally disparate demes along the species range (Woods Hole, MA; Montauk, NY; Metomkin Bay, VA; Wassaw Sound, GA; St. Mary's Sound, GA). Analysis of variance among and between deme means revealed variation in three specific shell characteristics: spire height, spinosity and shell thickness. Spire height was measured by the ratio of shell length to aperture length. Spinosity was determined as the ratio of the shell width including spines to the shell width excluding spines. Shell thickness was described by the regression line of the power function relating shell weight to shell length ($Y = aX^b$).

Spire height was greatest in northernmost and southernmost populations. Spinosity and shell thickness both changed in a N–S direction, with the Woods Hole deme having the smallest spines and the thinnest shells and the St. Mary's Sound deme having the largest spines and the thickest shells. ANOVA of the three characteristics revealed significant population differences. Comparisons of spire height were significantly different except between the Montauk and Metomkin demes, and all spinosity means were significantly different except between the Woods Hole and Montauk demes. Bonferroni's method of simultaneous comparisons between population shell thickness indicated no significant differences.

The observed morphologic variation closely fits the classic description of a cline. The hypothesized clinal variations are discussed in relation to physical and biological selective pressure gradients from across the species range. Sediment type and predation pressure are believed to be particularly important aspects of the species habitat.

GROWTH AND MOVEMENT OF OFFSHORE POPULATIONS OF *BUSYCON CARICA* AND *B. CANALICULATUM* AS EVIDENCED BY MARK AND RECAPTURE RESULTS

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Knobbed (n = 9,317) and channeled whelks (n = 485) were tagged and released from July 20, 1982 to October 23, 1984. Marked individuals were held overnight and returned to the collection area. Recaptures (n = 457) through March 1, 1987 indicate little movement (1.0 nautical miles) and limited growth. Shell length increases (1.0 mm per month) were greatest in tagged animals with an average SL of 98 mm. Absolute and relative allometric characteristics will be compared with data from studies of other long-lived gastropods. Growth curves for each species and major size category will be discussed.

STRESS, ACCLIMATION, AND SEASONAL CHANGES IN DEFENSE-RELATED OYSTER HEMOCYTE ACTIVITIES

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Oyster hemocytes play a major role in defense against parasites and diseases. Certain defense-related hemocyte activities, such as spreading to an ameboid shape and rate of locomotion, were found to differ in their response to acute and short-term salinity and temperature changes depending on the environmental conditions of their original habitat. In a high rainfall year (1984), the salinity of the Choptank River (Chesapeake Bay) reached 6–8 ppt. Oysters collected during this period had retarded hemocyte activities when tested *in vitro* at higher salinities. In 1985 however, there was less rainfall, salinities were 13–14 ppt and hemocyte activities were retarded by lower *in vitro* salinities. The activities of hemocytes from oceanic oysters remained consistent in both years, probably a result of the more constant environment. Temperature studies showed a dramatic difference between the two habitats in terms of hemocyte spreading characteristics, an occurrence that is still being investigated.

To document the seasonal changes, a monthly monitoring program was initiated to assay hemocyte activities after acute salinity changes, after week-long temperature/salinity stress, and during salinity acclimation. These results demonstrate the environmental influence over defense-related hemocyte activities.

POTENTIAL HAZARDS OF *DINOPHYSIS* TO CONSUMERS AND SHELLFISHERIES

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Diarrhetic Shellfish Poisoning (DSP) is a global public health problem which threatens the full utilization of valuable shellfish resources. Human illness results from the ingestion of shellfish which have fed upon toxic species of the planktonic genus *Dinophysis*. It is only in the last decade that extensive work by numerous researchers has identified the symptoms, toxin, and etiologic agents. A further complication in some geographic areas is the concurrent appearance of toxic *Dinophysis* species with the toxic dinoflagellate *Protogonyaulax tamarensis*, causative agent of paralytic shellfish poisoning (PSP). This can add to the severity and range of symptoms in the patient. It also adds to the difficulty of monitoring efforts and closure decisions relating to the shellfish growing waters. To adequately protect the consumer, monitoring of toxic species must be added to routine bacteriological standards for shellfish growing area closures.

Due to recent recognition of DSP, many past food-related incidents have been falsely attributed to bacteria, viruses, or unknown causes. Retrospective epidemiologic investigation of Nassau County shellfish-related illnesses have identified incidents which can now be reclassified as "probable DSP", based upon symptoms, as well as known seasonal and spatial distribution of *Dinophysis* as shown by plankton monitoring.

Results of monitoring in Nassau County waters have shown thirteen species of *Dinophysis* to be present; often several occur together. Frequency and abundance are greater in spring and summer, and in south shore waters, especially the ocean.

SEASONAL MICROSTRUCTURE OF THE INNER SHELL LAYER AND GROWTH RATES OF *GEUKENSIA DEMISSA* AT TWO INTERTIDAL LOCATIONS IN NEW JERSEY

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The microstructure of the inner shell layer of the ribbed mussel, *Geukensia demissa*, collected from two intertidal sites in New Jersey (Cape May near the mouth of Delaware Bay and at Bivalve near the mouth of the Maurice River), varied seasonally with an annual pattern consisting of prismatic structures formed in spring and early summer, nacreous tablets in late summer and early fall, and prisms again in late fall and early winter. Granular structures, which apparently resulted from dissolution of the inner shell layer by acidic end-products of anaerobic metabolism, were evident along the inner shell layer growth surface in winter and early spring at both sites. Dissolution of the inner shell layer growth surface was both more common among individuals and more pronounced within shells of mussels from Bivalve, which has a lower mean and greater range in salinity than Cape May. In spring and fall, variation in inner layer growth surface microstructure both between individuals at the same site and even on different parts of the inner shell surface of the same individual was quite large. Some of this variation among individuals was correlated with age. Despite differences in inner shell layer microstructure, growth rates at the two sites were similar and averaged approximately 12 mm in length per year for the first four to five years of life. Mussels as old as 15 years were collected.

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SIZE VARIATION IN MITOCHONDRIAL DNA OF *PLACOPECTEN MAGELLANICUS*

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The mitochondrial genome of *Placopecten magellanicus* is about twice as large as that of other metazoans, commonly measuring about 34.5 kilobase pairs (kb) but varying incrementally from about 32 to 39 kb. Most of the size variation can be accounted for by difference in copy number of a 1.2 kb tandemly repeated element. Digestion of scallop mtDNA with the restriction endonuclease Eco RI produces three invariant fragments and a fourth which brackets the repeat region and falls into seven discrete size classes, from 8.2 to 15.4 kb. In order to test whether mtDNA size could be a useful character in population discrimination, the mtDNA of 220 individual scallops from five geographic populations in the Maritime Provinces was digested with Eco RI and scored for variable fragment size. Differences in size class distribution were significant between the Baie des Chaleurs population and both the Eastern Shore and George's Bank populations. The frequency of a single size class, 9.4 kb, may prove to be useful as an indicator of population differences. Support by an NSERC operating grant to E.Z.

GENETIC IMPROVEMENT OF CULTURED BIVALVE SPECIES

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The promise of modern genetic techniques such as polyploidy, gynogenesis and 'genetic engineering' has aroused great interest in the application of genetics to molluscan mariculture. However, the full potential of these approaches will not be met if the basic groundwork is not laid. Essential prerequisities to more advanced genetic manipulations include the biological characterization of cultured species and the implementation of hatchery methods necessary to domesticate essentially wild species.

Mytilus in North America comprises three genetically distinct "species," which may differ significantly in terms of commercially important traits. Hatchery production of seed from these types and their hybrids could help to overcome regional problems such as summer mortality or particular diseases.

In mass spawning, a common means of obtaining bivalve larvae in hatcheries, the actual effective parental population size is well below the number of parents shedding gametes. This will lead to a limited representation of the natural gene pool in the larvae produced, as well as inbreeding in hatchery lines. Parental representation in progeny of mass spawnings may be assessed by electrophoretic analysis. Data from large and small mass spawnings of *Mytilus* and their implications for hatchery practice are discussed.

The ability to identify the parents of mass-spawned progeny reared in common allows more accurate quantitative genetic analyses and enhances the efficacy of family selection, by eliminating the environmental variation common to members of a family when families are reared separately. A preliminary quantitative genetic analysis of growth in *Mytilus* is presented.

In practice, broodstock are often selected with little attention to genetic considerations. Simple non-technical approaches to obtaining genetically superior broodstock are discussed.

PHYSIOLOGICAL EFFECTS OF *PROTOGONYAULAX TAMARENSIS* ON BIVALVE MOLLUSCS

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The effects of *Protogonyaulax tamarensis* (clone GT429) on shell valve and siphon activity, clearance rates, oxygen consumption, and cardiac activity were measured in 8 species of bivalves. After exposure to GT429, shell valve and/or siphon closure was: unchanged in *Mytilus edulis* (from Maine), *Spisula solidissima*, *Artica islandica*, and *Modiolus modiolus;* increased in *Mercenaria mercenaria*, *Ostrea edulis*, *Placopecten magellanicus*, *Geukensia demissa*, *Mya arenaria*, and *Mytilus edulis* (from Rhode Island). Clearance rates: increased in *Mytilus* (Maine), and *Ostrea;* were unchanged in *Mytilus* (Rhode Island), and *Spisula;* decreased in *Mercenaria*, *Geukensia*, and *Mya*. Oxygen consumption: increased in *Mytilus* (Rhode Island), and *Mya;* was unchanged in *Mytilus* (Maine); decreased in *Placopecten*. Cardiac activity was unchanged in *Spisula*, *Mercenaria*, *Artica*, and *Placopecten*. There was a transient decrease in heart rate in *Mya* after exposure to GT429; this was correlated with increased siphon closure. There were significant changes in cardiac activity in *Ostrea* (22% of individuals tested), *Geukensia* (60%) and *Mytilus* (57%). These changes were: increased heart rates, in *Geukensia* and *Mytilus;* periods of cardiac arhythmia: decreased heart rates.

THE GIANT SCALLOP (*PLACOPECTEN MAGELLANICUS*) FROM THE LOWER NORTH SHORE OF QUÉBEC: BIOLOGICAL CHARACTERISTICS AND AQUACULTURAL POTENTIAL

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The first raising experience, between 1980 and 1984 with spat imported from Newfoundland, permits us to identify the aquacultural potential of the species in this area. The results were good, and the Quebec government has been conducting research projects with the objective of studying the biological characteristics of the giant scallop in this inshore habitat.

Spawning occurred in July, which corresponds to the earliest complete spawning period mentioned for the species. This early spawning period, added to a favorable environment, permits a growth rate among the fastest described for the species, with certain individuals of the natural population attaining a size of 100 millimeters (4 inches) in 3½ years.

However, the collection of spat remains problematic, presumably because of the low densities of the spawners which have survived the overfishing.

As an approach to aquaculture of sea scallops, it is suggested that spat be produced in a hatchery nursery and placed in natural habitats. Ultimately, commercial collection of spat may be possible if spawning is successful and the sites chosen have a high retention of larvae.

DEVELOPMENT OF NURSERY TECHNIQUES FOR REMOTE-SET LARVAE OF *CRASSOSTREA VIRGINICA* IN VIRGINIA

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Studies are being carried out to test the remote setting technique for eyed larvae of the American oyster, *Crassostrea virginica*. Hatchery-reared eyed larvae (>202 μm shell length) were collected on a sieve, wrapped in damp Nitex and paper towels, and refrigerated at 5°C. Larvae were set on oyster shell, French tubes, and "Minicultch" (crushed oyster shell). Clean, aged oyster shells were bagged in 13" lay-flat vexar netting with 100 shells per bag. French tubes were aged and assembled in modules of 41 tubes.

After setting, the shell bags were placed at seven nursery sites along the York River in intertidal and subtidal zones using a variety of on bottom and suspension techniques. French tubes were put at three sites. Site, tidal zone, and time of planting were found to influence growth and survival of spat. Intertidal sites proved to be more effective for both shell bags and French tubes because of less fouling and crab predation. Spat did not survive at any subtidal site without air-drying of fouling three times a week. Survival of spat was greater for intertidal bags placed on the bottom compared to suspended intertidal bags. Mortality of spat was greatest during the first month at all nursery sites. Growth of spat was significantly greater for those set in June. In three months oysters were larger than 20 mm in shell length. Bags were then opened and spat put on grow-out grounds. Oysters were left on French tubes for grow-out.

PRELIMINARY RESULTS OF A STUDY OF THE RELATIONSHIP BETWEEN REPRODUCTIVE DEVELOPMENT OF THE QUAHOG (*MERCENARIA* SPP.) AND INFLUENTIAL PHYSICAL FACTORS IN THE INDIAN RIVER LAGOON, FLORIDA

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Although the northern quahog (*Mercenaria mercenaria*) exhibits a distinctly cyclical pattern of gonadal development throughout most of its range along the eastern seaboard of the United States, little information is available for the species at the southern limit of its range. Discernment of the reproductive cycle in Florida is complicated by the occurrence of *Mercenaria campechiensis* and hybrids in this region. The present study provides preliminary data on the reproductive cycle of *Mercenaria* spp. in the Indian River Lagoon and attempts to relate this cycle to potentially influential physical factors.

Hard clams were collected monthly from September 1986 to June 1987 in two geographically distinct areas of the Indian River Lagoon. Temperature, salinity, dissolved oxygen and chlorophyll concentration were monitored biweekly during this same time period. Hard clams of a variety of size classes were collected from three stations in each area, sectioned for histological examination, and classified according to developmental stage based on the visual appearance of the gonads and average monthly oocyte diameters. The relationship between reproductive development and potentially influential physical factors is discussed.

A COMPARATIVE ANALYSIS OF LARVAL AND EARLY POSTLARVAL SHELL MORPHOLOGY OF THE HARD CLAMS *MERCENARIA MERCENARIA*, *MERCENARIA MERCENARIA TEXANA*, AND *MERCENARIA CAMPECHIENSIS*

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Adults were spawned in the laboratory and resulting larvae were reared to an early juvenile stage (1 mm shell length). Larvae were reared at a density of 2 per ml in μm filtered, UV-treated seawater and fed a diet of Tahitian strain *Isochrysis galbana*. Temperature was held constant at 28°C ± 2°C and salinity remained constant at 28 ppt. Scanning electron photomicrographs were used to compare ontogenic changes in shell morphology.

Prodissoconch I and II length and height and larval hinge structure did not appear significantly different among offspring of the three parental types. *Mercenaria campechiensis* larvae appeared to exhibit increased external shell sculpturing and increased shell depth at late larval and early juvenile stages.

THE RELATIVE EFFECTS OF SESTON FLUX AND SEDIMENTS ON INDIVIDUAL GROWTH RATES OF *MERCENARIA MERCENARIA:* RESULTS OF A FACTORIAL FIELD EXPERIMENT

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Preliminary descriptive/correlative field studies on wild *Mercenaria mercenaria* in a coastal lagoon in southern New Jersey suggested that individual growth rates are affected by "food provision rate" (equivalent to the horizontal flux of seston; flux units mg seston/cm^2/s) and deposited sediments. Based on these findings a 3 × 3 × 3 factorial field experiment (3 sites, 3 sediment types, 3 replicates of each treatment plot) using hatchery-reared clams was run from May–Sep 1986 to determine relative effects of seston flux and sediments.

Ten clams (30–45 mm length) were placed in each of 36 (12 per site) experimental plots, each a round excavation 0.3 m^2 area and 10–15 cm deep in the ambient sediment filled with either mud, sandy mud, or sand; clams were also put in undisturbed sediment at each site as controls for the sediment transplant procedure.

An ANOVA, with change in shell length as the dependent variable, showed significant differences between sites ($P < .001$) and sediment type ($P < .05$).

Combining all data by site and sediment type showed a 13% difference in growth rates between the slowest and fastest sites, and a 6% difference between sediment types, with slowest growth in mud and fastest in sand.

Tidal current velocities and four seston parameters (chlorophyll *a*, particulate inorganic and organic matter [PIM and POM], and energy content) were measured >20 times in near-bottom waters at each site. Flux of POM was well-correlated with growth rates. Neither seston concentrations nor current velocities alone were correlated with growth rates. Hence, the significant "site" differences are attributed to differences in seston flux.

This experiment provides further support for the importance of seston flux in controlling growth rates of suspension-feeding bivalves. It also provides the first estimate of the relative importance of seston flux and sediment type.

SUSPENDED CULTURE OF THE MANGROVE OYSTER, *CRASSOSTREA RHIZOPHORAE* IN JAMAICA

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The heavy fishing pressure on the wild mangrove oysters, *Crassostrea rhizophorae*, in Jamaica has led to the decrease in natural populations. Recent efforts of the Ministry of Agriculture with the assistance of the International Development Research Centre (Canada) has resulted in the establishment of commercial culture of this species in several area of Jamaica. Seed oysters are collected on pieces of reject tires at Bowden, St. Thomas in intertidal racks. After 6 to 8 weeks at a size of about 2.5 cm the seed are sold to the farmers who grow them suspended from 10 m × 10 m rafts or from longlines, depending on the site. Within another 5 months the oysters are harvested and sold to local vendors or restaurants. Although the harvest size is small (50 to 60 mm) and mortality is high (up to 80% during growout) the demand is high and prices are high resulting in good incomes for the farmers.

THE ORIGIN, EVOLUTION AND ZOOGEOGRAPHY OF BUSYCONINE WHELKS

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Although never rich in number of species, the subfamily Busyconinae has been a conspicuous component of the marine gastropod fauna of eastern North America through most Cenozoic time. Analysis of recent and fossil busyconines has shown that the subfamily is divisible into 9 groups, each spanning comparatively short intervals of geological time, and consisting of one or a very few lineages that are divisible into chronospecies. Examination of the distribution of these groups through time and space suggests that busyconine evolution can best be characterized as a stochastic accumulation of minor morphological changes brought about by genetic drift resulting from vicariance or competitive exclusion from portions of the habitat. Major events in busyconine evolution correlate well with major climactic changes throughout the Cenozoic.

The anatomical organization of busyconines is similar to that of other Buccinacea except for modifications of the alimentary and reproductive systems. The degree of anatomical differentiation between lineages correlates well with time since divergence.

EFFECT OF DOCOSAHEXAENOIC ACID ON GROWTH AND FATTY ACID COMPOSITION OF THE LOBSTER, *HOMARUS AMERICANUS*, AND THE BIOCONVERSION OF (1-^{14}C)-LINOLENIC ACID TO HUFA'S

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A two phase study was conducted over 3 years to clarify the essential fatty acid (EFA) requirements and metabolism of the lobster, *Homarus americanus*.

In Phase I, juvenile lobsters were reared for four months at 20°C and fed purified diets supplemented with 9% HCO (hydrogenated coconut oil) or 8% HCO and either 1% 18:2n6, 1% 18:3n3, 1% 22:6n3 or 1% of one of four mixtures of these purified fatty acids. Fat-free and reference diets were also tested. Diets containing 22:6n3 promoted significantly greater growth than *all* other diets. Whole body fatty acid composition indicates a low bioconversion rate of 18:3n3 to n3 HUFA's (highly unsaturated fatty acids).

In part of Phase II, the influence of EFA status on the capacity for bioconversion of 18:3n3 to 20:5n3 and 22:6n3 was examined. Juvenile lobsters were reared for 6 months on purified diets containing 8% oleic acid (18:1n9) and either 1% 18:3n3, 1% 18:2n6 or 0.75% 18:3n3 + 0.25% 18:2n6. EFA-free and reference diets were tested for comparison.

Injections of (1-^{14}C) 18:3n3 were made into 3 intermolt, post-absorptive lobsters/diet treatment. The proportional distribution of ^{14}C-labeled tissue specific polar and neutral fatty acids was analyzed.

This paper discusses the ability of juvenile lobsters reared at 20°C for bioconversion of 18:3n3 to HUFA and the implications for dietary requirements.

CHARACTERISTICS OF INBRED OYSTER STRAINS SELECTED FOR RESISTANCE TO *HAPLOSPORIDIUM NELSONI* (MSX)

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A project to develop oysters resistant to mortality caused by the parasite *Haplosporidium nelsoni* has been underway at Rutgers University since the early 1960s. Strains were begun from wild stocks originating in several locations along the east coast of the United States, including Long Island Sound, the Navesink River (New Jersey), Delaware Bay, and the James River (Virginia). Most of the lines have been produced through inbreeding and we now have 6th and 7th generations in some strains.

Although survival has increased on the *average* with increasing selection (mean survival of 5th generation groups is 10 times greater than that of unselected controls), performance of *individual* strains has been less clear-cut. Unexpectedly large parasite-associated mortalities have occurred in some highly selected groups. Such failures are not correlated with degree of inbreeding, as measured by estimated inbreeding coefficients, and preliminary results indicate that outcrossing does not significantly improve survival.

Despite intense selection through several generations in Delaware Bay, strains originating in Long Island Sound and in Virginia still follow reproductive cycles that are characteristic of the original wild populations. Long Island oysters ripen and spawn at lower temperatures than those from Delaware Bay, which, in turn, ripen at lower temperatures than Virginia strains. Also, growth rates of inbred Long Island groups remain higher than those of Delaware Bay groups, as is the case of the parent wild stocks.

Results suggest a continued strategy of inbreeding to improve resistance and to maintain other characters. Crosses could then be employed to try to blend two traits such as fast growth and high resistance.

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GROWTH OF GEORGIA *MERCENARIA MERCENARIA* (L.) JUVENILES IN AN EXPERIMENTAL DOWNWELLER SYSTEM

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As part of a Georgia Sea Grant funded project (genetic selection for fast growth) five cohorts of *Mercenaria mercenaria* (L.) seed were stocked at various densities (0.3–3.3 Kg/m^{-2}) on experimental scale downweller systems and growth was analyzed for the period October 15 to December 1, 1986. To ensure the maintenance of each cohort's inherent genetic variance, seed were never graded or separated according to size. The mean flow rate to

the downwellers was 1.2 L/min^{-1}, with the ambient water supply (sand filtered) being replaced daily for *ca.* 6 hours by cultured sea water (Wells Glancy Method) at the same mean flow rate. Mean biomass increases varied among downwellers from 130.6–954% in the 47 day period. Flow rate to biomass ratios are shown to have a great effect on growth rates. Flow rate to biomass ratios varied from 11.6–72.8 $L/min^{-1}/Kg^{-1}$. A doubling to trebling of biomass was achieved within the flow rate: biomass range of 14.1 to 17.2 $L/min^{-1}/Kg^{-1}$, after 47 days. These figures are very similar to the results reported by Manzi *et al.* (1986) for experimental scale upweller systems in South Carolina. Cohorts can be divided into groups which grew faster in the first (Oct. 15–Nov. 11) or second "half" (Nov. 11–Dec. 1) of the study period. Growth rates achieved by these groups were shown to be significantly different during the second "half" and are thought to be dependent on the flow rate to biomass ratio.

GENETIC IMPROVEMENT OF THE PACIFIC OYSTER (*CRASSOSTREA GIGAS*) FOR COMMERCIAL PRODUCTION

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There are very few examples of the direct application of genetics to the commercial production of bivalves. The recent employment of the induction of triploidy by the Pacific oyster industry suggests a recognition of the role of genetic technology. However, genetic approaches to the improvement of stocks have not been incorporated into the routine production of seed stock.

Genetic research at the University of Washington has investigated several approaches to the enhancement of production traits in Pacific oysters. First, a selection and breeding approach developed stocks of oysters resistant to summer mortality. These stocks have only been minimally employed in commercial production. As a "side benefit" of this program, lines were produced that exhibited increased levels of glycogen, compared to natural, or non-selected hatchery stocks. Further genetic work with this trait indicated it is highly heritable and could potentially be valuable to increasing product quality.

The second approach used has been interstock breeding to determine the influence of heterosis on growth and other production traits. Four genetically divergent stocks were crossed in a 4 × 4 factorial mating design, which was replicated once. The progeny from these crosses were planted in four differential environments and were analyzed for growth traits. Results suggest that genetic differences are consistent over environments, although there are some genotype X environment interactions. Additionally, heterosis was exhibited for some growth traits in several crosses. The data indicate that interstock crosses may be a valuable approach to initiating a broodstock and that crossing of specific stocks for production may be a beneficial technique to incorporate into commercial operations.

OVERWINTERING AMERICAN OYSTER (*C. VIRGINICA*) SEED BY COLD DAMP AIR STORAGE

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Seed oysters of 8 to 12 mm size were held in damp dry conditions at 0, 3 and 6 degrees Celsius for 1 to 5 months from 1 January to 30 May 1986. Surprisingly those damp stored the longest (4 and 5 months) had the greatest survival (over 90% compared to 60 to 70% for those placed earlier in ambient seawater). The reason for this is not clear however conditions of temperature and food in ambient seawater were thought to be controlling factors. Current trials are with larger 50 mm seed oysters. These results have immediate application in the efficient winter storage of hatchery seed stocks and may point the way to overcoming winter predation losses in aquaculture field operations.

QUANTITATIVE AND SINGLE-LOCUS GENETIC ANALYSIS OF PRODUCTION IN BIVALVES

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Variation in phenotypic traits such as production characteristics may be studied using either quantitative or single locus genetics. Single locus studies typically focus upon the evolution of electrophoretically detectable polymorphisms and are usually assumed to explain only a minor fraction of the variation in phenotypic traits. Quantitative genetics on the other hand can be used to

demonstrate that some fraction of the variation in a trait is genetic in origin but yields virtually no insight into the action or identity of the genes influencing these traits. In this study we test the feasibility of combining single locus and quantitative genetic analysis into a single study of growth in marine bivalves. The ultimate goal of this research program is to determine the magnitude of genetic variation for production traits then to attribute a portion of this genetic variation to the action of specific gene loci.

Genetic variation at the *Lap* locus in *Mytilus edulis* has been demonstrated to have a profound influence on the physiology of mussels in natural populations. Here I demonstrate that this locus also explains a significant proportion of the variation in growth and reproductive output. Maximum heritabilities for physiological traits were determined using a repeatability analysis. Taken together these data indicate that the *Lap* locus explains virtually all of the genetic variation in these physiological traits which affect growth. A second analysis of juvenile growth rate in the hard clam *Mercenaria mercenaria* is underway and will also be discussed.

SMALL SCALE SHELLFISH HATCHERY: DESIGN MANUAL

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A manual was prepared which outlines the processes and equipment required to culture four shellfish species (i.e. American oyster, European flat oyster, Bay quahaug and Bay scallop). The methods of producing food for the shellfish (i.e. culturing algae) are also presented. An energy-efficient design for the hatchery building was developed which is simple and lends itself to residential construction methods (e.g. a prefabricated building system). The hatchery was designed for a minimum production of 200,000 seed per species. However seed production could be increased substantially by using larger tanks to rear larvae and installing an outdoor nursery.

DUNGENESS CRAB MEGALOPAE ABUNDANCE OFF THE WEST COAST OF VANCOUVER ISLAND IN RELATION TO OCEANOGRAPHIC EVENTS

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Larval Dungeness crab (*Cancer magister*) abundance in the waters off Vancouver Island was monitored in 1986 to define spatial patterns of abundance in ongoing studies of factors affecting year class strength. In contrast to 1985, when only one transit line was monitored monthly, in 1986, a number of lines were completed over a two week period.

Megalopae were found to be concentrated further offshore in 1986 than in 1985, although they again appeared to be concentrated in the boundaries between opposing currents. Ocean drifters were used to establish surface current patterns and to allow continuous sampling of a specified water mass over a 3-day period. Temporal occurrence of megalopae in surface water was better defined, with maximal abundance occurring at nautical twilight in the evening. Hypotheses involving oceanographic and meterological events are discussed in relation to observed fluctuations in year class abundance in inshore waters.

SPATIAL PATTERNS OF MUSSEL GROWTH AND SURVIVAL THROUGHOUT BRITISH COLUMBIA

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Mussels were cultured at 18 sites throughout British Columbia, ranging from southern Vancouver Island to the Queen Charlotte Islands. Indigenous mussels were cultured at each site, with 62% of the mussels at each site individually tagged. Growth and mortality was monitored every 6 weeks from May through October. Significant differences in growth and survival were found between sites, and the pattern of these differences is discussed as to its implications for mussel culture in British Columbia.

THE EFFECTS OF AGE, SIZE, AND STOCKING DENSITY ON SURVIVAL AND GROWTH OF *OSTREA EDULIS*

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A tremendous variation in size of the European oyster at almost any age and in any environmental condition is recognized as one of the most important problems affecting both aquaculture and selection programs of this species. In this study, the effects of the environmental factor stocking density, on survival, growth rate and growth variation of three year classes of oysters (i.e. 1983, 1984 and 1985) were studied. Three discrete size groups of the 1983 and 1984 year classes were graded, whereas two discrete size groups were used for the 1985 year class. Three stocking densities plus a control for the 1983 and 1984 year classes and two stocking densities plus a control for the 1985 year class were used. The animals parameters—length, width and weight—were monitored over two growing seasons.

With increasing stocking density, growth rate was retarded whereas growth variation was increased. Where the animals of three size groups were grown together, the data tended to show that growth rate was retarded only in the animals of the small size groups. This non-random effect is discussed as well as possible applications to aquaculture and selection programs.

MEASURING THE ECONOMIC EFFECTS OF BROWN TIDES

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This paper develops behavioral models for examining the reactions of marine resource users to reduced resource quality associated with brown algal blooms. Models of recreational and commercial fishing are developed, as well as other recreational uses.

These models emphasize the concept that the presence of brown tides at certain sites will cause the substitution of other sites and other species. These substitutions will have additional implications for economic welfare.

After developing the conceptual models, preliminary estimates of economic losses for certain activities are generated. These estimates include shellfish in the Peconic Bays region.

IN VITRO STUDIES ON THE PARASITE, *HAPLOSPORIDIUM NELSONI* (MSX) AND THE BLOOD CELLS OF THE OYSTER, *CRASSOSTREA VIRGINICA*

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Moderate to heavy infections of *Haplosporidium nelsoni* (MSX) in oysters can be diagnosed with 93–100% accuracy using fresh blood preparations. A notch made in the oyster shell allows access to the adductor muscle sinus and approximately 0.5 ml can be easily withdrawn with a 1 ml glass tuberculin syringe and 25 gauge steel needle without sacrificing the oyster. A drop of blood is then placed on a slide without a coverslip and observed on an inverted microscope at 200× magnification. Oysters can be kept at 12–15°C in a chilled, circulating seawater system and may be re-bled numerous times to provide a continuous supply of hemocytes and parasites for experimental work. Length of survival for these oysters in the laboratory is inversely related to infection intensity and the infection frequently progresses to an advanced stage before the oyster dies.

Initial flow cytometry studies indicate two oyster cell populations: lower density, lower volume cells presumed to be hyalinocytes and higher density, higher volume cells thought to be granulocytes. Although usually larger than oyster hemocytes, MSX shows much more variation in size and density range and smaller MSX overlap with granulocytes to a certain degree. Comparisons of MSX-infected and uninfected blood show differences in the ratios of oyster cells relative to MSX infection. Changes in the physical appearance and properties of MSX and oyster hemocytes have also been noted possibly in response to seasonal or environmental stimuli. Unusual, non-spherical MSX that appear to be in a rapidly dividing state and exhibit limited movement occur during the warmer months from spring through early autumn.

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HARD CLAM (*MERCENARIA MERCENARIA*) ABUNDANCE IN EASTERN GREAT SOUTH BAY, LONG ISLAND, NEW YORK: POPULATION DISTRIBUTION AND STRUCTURE

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Hard clam (*Mercenaria mercenaria*) populations can be characterized by distinct areas of high clam abundance surrounded by areas of lower clam abundance. This distributive pattern has been related to environmental differences, particularly bottom type. Little attention, however, has been given to the hard clam population structure of high and low density areas. Such information could yield insights into the forces influencing abundance which can in turn, have important fishery management implications.

In 1986, the Town of Brookhaven undertook a hard clam population survey of eastern Great South Bay, an area of 3238 hectares, that in 1985 produced 40,000 bushels of hard clams. Replicate 1.02 meter^2 grabs were taken at 140 stations according to a block random design with 1.7 × 10^5 meter^2 quadrants.

Length and thickness of all clams greater than 20 mm in length was measured. A hard clam distribution map was prepared using a 5 cm per meter^2 (apparent minimum density for harvesting) cutoff. Five distinct areas (beds) having densities greater than the cutoff and 3 areas with densities below the cutoff (nonbeds) were identified. Size (age) frequency distributions were calculated bay-wide and for each bed and non-bed.

Bottom type in beds was sand or muddy sand with shell fragments while non-beds had muddy sand or mud without shell fragments. The population structure was similar for beds and non-beds even though the mean density of all beds and all non-beds was 10.6 and 2.4 clams per meter^2 respectively; both had annual recruitment. However, individual bed stations had a greater range of sizes than did non-bed stations. This suggests that the population dynamics in beds and non-beds are different. Field, laboratory and literature data provide some insight as to causes. Management implications are considered.

EFFECTS OF THE "BROWN TIDE" ALGA ON BIVALVE FEEDING

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A picoplanktonic algal bloom, attributed to the chrysophyte *Aurecoccus anorexefferens* (2 μm in diameter), caused severe reduction in tissue weights of adult bay scallops and recruitment failure of the 1985 year class in Long Island's embayments. To determine the causes of these adverse effects, the feeding mechanisms of adult bay scallops, *Argopecten irradians irradians*, and mussels, *Mytilus edulis*, on this alga were compared in terms of clearance rates, retention efficiencies and absorption efficiencies. Clearance rates for *Aureococcus* at the peak of the bloom (2×10^6 cells/ml) were about an order of magnitude lower than those for a control diet of the diatom *Thalassiosira weissflogii* at optimal cell concentrations. Laboratory grazing studies using field collected water samples enriched with *Thalassiosira* cultures (11 μm in diameter) demonstrate that scallops retain *Aureococcus* with low efficiency (36%) relative to mussels (59% efficient). Preliminary results using the twin ^{15}Cr:^{14}C radiotracer technique and laboratory cultures of *Aureococcus* indicate that at low algal densities scallops are able to absorb the "brown tide" alga with high, greater than 85%, efficiency. This is consistent with the lack of a rigid cell wall in this algal species. These results suggest that the negative impact of the "brown tide" on adult scallops is not caused by indigestibility of the alga, but can be at least partially attributed to the combined effects of depressed feeding and absorption rates at high cell densities and poor retention of *Aureococcus*.

THE GROWTH OF THE GIANT SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*) IN THE SOUTHERN GULF OF ST. LAWRENCE

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Giant sea scallops were sampled during a period of 4 years (1982 to 1985) from three areas of the southern Gulf of St. Lawrence: Baie de Chaleur and the central (Borden/Cape Tormentine) and western (Pictou Island) sections of the Northumberland Strait. The shells were measured and aged using the annual rings.

The data were fitted to the Von Bertalanffy growth equation for the three areas. Geographical variations were detected, with the fastest growth in Baie de Chaleur and the slowest growth in the western section of the Northumberland Strait.

These results may indicate the existence of subpopulations. The implications of the results to fishery management are discussed.

THE FEASIBILITY OF CULTURING THE EUROPEAN OYSTER, (*OSTREA EDULIS*), ON THE BOTTOM, IN NOVA SCOTIA

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The feasibility of rearing the European oyster, (*Ostrea edulis*), on the bottom, for part or all of the culturing period was examined both in the laboratory and the field. Four size classes of oyster were used, (19–38 mm, 38- 62 mm, 62–75 mm and 75–100 mm in diameter), each representative of a successive oyster size class. In the field, oysters were placed both within and outside fenced enclosures on the bottom, as well as in nets suspended at the surface. This enabled testing for differences in growth, and natural and predator induced mortality. The laboratory experiments were established in order to test the two main oyster predators, *Homarus americanus* and *Cancer irroratus*, for an optimal prey size and a critical prey size.

Preliminary field results indicate that while growth rates are

higher at the surface than on the bottom, and mortality rates lower, the difference decreases with increasing oyster size.

In the laboratory, selective predation, by both lobsters and crabs, on the smallest oyster size classes was observed.

Both field and laboratory results will be discussed in greater detail.

HISTORICAL TRENDS IN THE SHELLFISHERIES OF RARITAN BAY (NEW YORK, NEW JERSEY)

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During the 1800s and early 1900s, Raritan Bay had commercial fisheries for five shellfishes: (1) oyster, *Crassostrea virginica*, (2) soft clam, *Mya arenaria*, (3) hard clam, *Mercenaria mercenaria*, (4) blue crab, *Callinectes sapidus*, and (5) lobster, *Homarus americanus*. Since then, the oyster and soft clam fisheries have ceased to exist and the hard clam, blue crab and lobster fisheries have had periods of substantial decline.

Because the oysters became polluted the fishery, which had been the largest of the five, gradually declined after about 1910; operations ceased permanently in 1925.

The soft clam fishery was substantially curbed in the late 1930s when the intertidal flats became polluted. At the same time, however, a wasting disease killed the eelgrass, *Zostera marina*, in the bay; as a result, soft clams became scarce on the flats. In 1950, subtidal clamming areas of the bay were closed to fishing due to pollution.

The hard clam fishery was also limited by pollution and increasingly smaller areas of the bay were open for marketing the clams. The entire bay was closed in 1961. The eastern end of the bay has been reopened for fishing since 1983 when a depuration plant was constructed to process hard clams. These clams can be and have been relayed to clean beds in Barnegat Bay.

The winter dredge fishery for blue crabs has continued into the 1980s but landings have fallen. Daily catches per boat are substantially lower in the 1980s than they were in the 1920s and 1930s.

The lobster fishery continued into the 1980s. Catches were extremely small from about 1955 to 1970, but have since increased somewhat.

VARIABLE GROWTH RATES OF SEED CLAMS, *MERCENARIA MERCENARIA*, IN AN UPFLOW NURSERY SYSTEM: CAN PRODUCTION COSTS BE DECREASED BY REMOVING SLOW-GROWERS

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Variable growth rates complicate efforts to culture marine bivalves. Normal operating protocols that include handling and sorting animals by size may provide an opportunity to identify slow growing animals and increase production efficiency by removing these animals from the culture system.

The growth rates (increase in shell length) of seven separate size classes of seed clams (*Mercenaria mercenaria*) isolated from a common cohort were monitored weekly in a commercial upflow nursery system from June 15 through September 9, 1986. Experimental results were input into a cost-analysis model to compare commercial production costs with and without culling.

There were significant differences in the growth rates of some size classes demonstrating the ability to use current relative size to predict short term relative future growth. Only size classes that were composed of a relatively small proportion of the total cohort representing the lowest end of the size distribution (smallest 15% or less) exhibited significantly reduced rates of growth, however, and initial growth periods of from 22 to 33 days in the nursery system were required before these slow growing size classes could be identified. Also, the difference between the growth rates of fast and slow growing size classes was not great since slow growing size classes achieved field size (6 mm) only a week or two later than faster growing size classes. The results of the cost-analysis model indicated that removing slow growing animals from the production system would not result in a net reduction in production costs since the value of the animals discarded exceeded the savings realized by confining production to fast growing individuals.

ANALYSIS OF GROWTH IN *MYA ARENARIA*, FROM LONG ISLAND SOUND, USING INTERNAL LINES

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In order to analyze growth, samples of a *Mya arenaria* population were collected bimonthly from July 1986 through June 1987. In these specimens, annuli on the external shell could not be discerned from lines possibly caused by spawning and environmental stresses; therefore external shell lines were not considered a reliable method for age determination. Growth lines in the chondrophore, an internal shell structure, proved reliable for age determination. Left valves were sectioned along a lateral line extending

from the umbo through the chondrophore to the ventral margin. Thin sections revealed distinctive annuli in the chondrophore. However, because of weathering and other environmental effects that eroded the external surface of the shell, height measurements at intermediate ages could not be obtained since annuli in the chondrophore could only occasionally be traced into the external shell.

To resolve the problem of obtaining height measurements at intermediate ages, height of each left valve and chondrophore length were measured for specimens of various sizes. A linear relationship between chondrophore length and valve height was established. Using this relationship and chondrophore length at each annuli, shell height and growth for each year of the clam's life can be estimated. This method was used to examine both annual and bimonthly growth in the Long Island Sound population. The linear relationship between valve height and chondrophore length provides a useful method for obtaining growth information for several years from a single specimen.

GENETIC ANALYSIS OF GROWTH AND VIABILITY IN THE BLUE MUSSEL, *MYTILUS EDULIS*

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Estimates of heritability and genetic correlation were derived from 30 half-sib groups, each having 3 replicated families, of the blue mussel *Mytilus edulis*. The additive genetic variance for shell growth was generally high at the larval and juvenile stages. Better hatchery performance could be achieved by selecting for faster larval growth and higher metamorphosis success through a progeny testing scheme. Given the positive genetic correlation between juvenile and adult shell growth, and the higher heritability at the juvenile stage, selection for post-larval growth could be conducted with animals less than one year of age.

THE RESPONSE OF SWIMMING AND METAMORPHOSING OYSTER LARVAE TO LOW DISSOLVED OXYGEN

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Portions of the Chesapeake Bay and its subestuaries periodically experience low dissolved oxygen events which are either concurrent with or partially overlap with the spawning season of the oyster *Crassostrea virginica*. In assessing the impact of such events two questions arise: how is oyster larval swimming activity influenced by low PO2, and how does sustained low PO2 influence success of metamorphosis to the attached benthic form? Larval swimming was examined using IR video while larvae were maintained in a flow-through chamber in which PO2 was controlled. Despite sequential decreases in PO2 from 100% to <9% saturation (at 20 ppt and 25°C) over a 3-hour period, no cessation of swimming was observed, i.e. larvae can maintain swimming activity at <0.5 ml/L O2. To examine metamorphosis, competent pediveliger larvae were exposed to sustained PO2 concentrations of 100, 20 and 5% saturation for periods of 2, 4, 6 and 8 days in the presence of a settlement substrate. A 2-day exposure at 20% saturation produces no apparent decrease in metamorphic success. Similar exposure at 5% saturation produces decreased metamorphosis; however, measurable metamorphosis is evident even after 8 days' exposure at 5% saturation. Larval oysters are clearly more tolerant of low PO2 than was previously suspected.

APPLIED BREEDING OF THE HARD CLAM *MERCENARIA:* GROWTH OF OUTBRED LINES FROM CROSSES OF SELECTED COMMERCIAL HATCHERY STOCKS

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A large-scale breeding program was initiated in South Carolina to achieve improved growth and survival of hard clams. Selected broodstocks from Aquaculture Research Corporation and Virginia Institute of Marine Science were spawned on three occasions at different times of year for production of both inbred and reciprocal outbred lines. Offspring were reared under identical conditions in the hatchery, nursery and field. Growth and survival were monitored at regular intervals for two years and the populations were sampled at one year of age to determine allozyme frequencies. In each of the trials, one of the outcrossed lines demonstrated more rapid growth than the parental lines, but it was not the same line in each case. Early growth was not a good predictor of subsequent growth. Early growth was strongly affected by the time of spawning, resulting in great disparities between trials. This differ-

ence, however, disappeared by the time the lines reached 18 months of age. There was some indication that the fastest growing lines were more heterozygous than other lines, but no relationship between heterozygosity and rapid growth could be demonstrated within lines. Some of the population reached market size in 18 months and a large portion were market size in two years from spawning, an increase of at least 6 months over grow-out expectations of South Carolina wildstock.

ENERGETIC IMPLICATIONS OF INDUCED TRIPLOIDY IN *MYA ARENARIA*: THE CONSEQUENCES OF AGE AND SEXUAL MATURITY

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Juvenile *Mya arenaria* were treated with cytochalasin B to induce triploidy and examined with respect to components of the balanced energy equation: C = P + R + E + G. Parameters measured were oxygen uptake, filtration rate, dry tissue weight, shell length, shell height and shell inflation. Energy budgets were constructed and diploid and triploid groups compared.

Because triploid adult bivalves reportedly grow larger and faster than their diploid siblings, the difference should be traceable to some difference in energy allocation. In one proposed mechanism, more energy may be available for somatic growth in triploid adults due to retarded gametogenesis. Another hypothesis states that the expected increase in heterozygosity should enhance growth, as measured by changes in the energy budget.

Very few significant differences were found between diploid and triploid juvenile clams (year 1, 10–20 mm). The differences became more pronounced in siblings during the next year of growth (25–40 mm). During the second year (sexually mature), differences were measured between the diploids and triploids and gametogenic progress was monitored.

It is suggested that juvenile triploid clams do not enjoy any energetic advantage over their diploid siblings and that the difference in growth rate found between the diploid and triploid individuals is a result of the blockage of gametogenesis in triploid individuals and the consequent reallocation of energy to somatic tissue.

STORM RELATED MORTALITY OF LOBSTERS, *HOMARUS AMERICANUS*, ON THE NORTHERN SHORE OF PRINCE EDWARD ISLAND, CANADA

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A late fall storm washed lobsters, *Homarus americanus*, upon the beach, which subsequently froze or were preyed upon. Five kilometers of beach were surveyed and an estimated mortality of 29 lobsters per linear kilometer was determined for the study area. Carapace length of the dead lobsters ranged from 22 to 135 millimeters. The occurrence of this type of weather related mortality should be considered in the context of natural mortality.

HABITAT PREFERENCE OF DUNGENESS CRAB, *CANCER MAGISTER*, IN PADILLA BAY, WASHINGTON

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Abundance and distribution of juvenile and adult stages of Dungeness crab, *Cancer magister*, were surveyed in Padilla Bay from May 1985 to August 1986. A 3 m beam trawl was used to sample 19 intertidal and subtidal channel stations. Commercial crab pots modified with small-mesh screen to retain smaller crabs were fished at 9 of the trawl stations. Diver transect surveys were conducted next to some of the trawls to help to quantify the catch efficiency of the beam trawl, and intertidal quadrat samples (0.25 m^2) were collected along 8 transects.

Habitat preferences for each of the age classes were different. Typically, 0+ (young-of-the-year) crabs (up to about 30 mm size) preferred intertidal or shallow subtidal areas with algae (especially *Ulva*) or eelgrass cover, although cobble and gravel substrates were also favored with or without plant cover. The 1+ age class (crabs entering their second year of growth) crabs preferred the shallow channels, moving out to the deeper channels as they grew to 2-year-old crabs. Gravid females were essentially absent from Padilla Bay, probably migrating to areas near deep water for mating and egg production.

A GENETIC COMPARISON OF *MACOMA BALTHICA* FROM SAN FRANCISCO BAY (CALIFORNIA) AND COOS BAY (OREGON), U.S.A.

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Macoma balthica specimens were examined at up to 12 enzyme loci using standard starch gel electrophoresis. Allele frequencies at each loci were compared among locations and to individual shell length within and among locations. It was found that the Oregon and California populations were drastically different at nearly all loci examined. These differences range from variations in allele frequencies to the occurrence of unique alleles at either population.

A previous investigation by Meehan (1985) revealed a similar level of genetic differences between eastern and western North Atlantic populations of *M. balthica*. The locus MDH-1 was clearly resolved in the western N. Atlantic specimens but not in eastern north Atlantic specimens. This same phenomenon occurs between Oregon and California specimens. A population from Virginia is currently being assayed for direct comparison of all twelve loci to Pacific populations.

In appearance, the *M. balthica* collected from Oregon are very similar to European *M. balthica* and those collected from California appear similar to western N. Atlantic specimens. Beukema and Meehan (1985) presented growth and other shell characteristics indicating differences between eastern and western North Atlantic specimens of *M. balthica*. Exchange of marine organisms from the western N. Atlantic to San Francisco Bay has occurred via ship ballast water and by more direct means with purposeful introduction of commercial species (Carlton 1985). It might be that the San Francisco *M. balthica* represent an introduced population from the western Atlantic. The Oregon population might be a natural extension of *M. balthica* from boreal regions and are more closely related to European *M. balthica*.

EXFOLIATIVE CYTOLOGY AND HISTOPATHOLOGY OF *GEUKENSIA DEMISSA* EXPOSED TO COPPER AT HIGH AND LOW SALINITIES

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The response of *Geukensia demissa* to copper (Cu) toxicity at high and low salinities was examined during exfoliative cytological and histological techniques.

Results of previous Cu dosing experiments showed that Cu effects on mussels were enhanced by increased salinity (using byssal thread attachment as a physiological assay). Similar salinity mediated responses were encountered by examining exfoliated cellular elements. Exfoliated cells of Cu exposed mussels were monitored throughout a 4-day Cu exposure (150 ppb) and 4-day recovery period at 10 and 30 ppt salinity. More hemocytes were exuded at the low salinity than at the high (2.6×), reaching a high of 15.5 vs 5.9 million cells/mussel/day. Sloughing of ciliated epithelial cells by Cu exposed mussels was 2.3× greater at 30 ppt than at 10 ppt salinity, attaining a maximum of 3.8 vs 1.0 million cells/mussel/day respectively. In the experimental mussels, Cu concentrations rose 3–4 fold in hemocytes from freshly drawn hemolymph as contrasted with increases of 20–30 times in exfoliated cells. These results indicate that the enhanced hemocyte exudation at low salinity may be a cellular mechanism by which excess Cu is eliminated, while sloughing of ciliated epithelial cells reflects damaged gill tissues.

Corroborative histological examination of mussels after 4-day Cu exposure revealed that intestinal epithelia and gill tissues were sites of hemocyte diapedesis. Hemocyte counts in intestinal epithelia rose by 289 and 80% in Cu exposed mussels at 10 and 30 ppt salinity, respectively. Copper exposed mussels had relatively more hemocytes in intestinal and rectal lumina than the controls. Gill filaments of Cu exposed mussels exhibited a high degree of tissue derangement, and were the most probable source of sloughed ciliated epithelial cells. Histopathological alterations were also noted in the digestive diverticula, plycate organs, kidney tubules, and bladders.

USE OF GONAD AREA/BODY AREA RATIO IN HISTOLOGICAL SECTIONS OF *CRASSOSTREA VIRGINICA* TO MONITOR REPRODUCTIVE DEVELOPMENT: RELEVANCY, DIFFICULTIES AND SOLUTIONS

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Seasonal changes in the reproductive development of bivalves have been usually described in terms of subjective stages in the development of their gonads and the gametes within. They have often been described quantitatively using volumetric stereological

methods as well as direct gravimetric measurements in species whose gonad can be excised separately from the rest of the body. Gravimetric and biochemical condition indices have also been used. Less often used has been the ratio of gonad area to total body area in histological sections. In bivalves such as *Crassostrea virginica*, whose gonad mass cannot be separated from the rest of the body, this ratio constitutes an alternative to direct gravimetric measurements. The gonad in oysters increases in thickness as the gametogenic cycle progresses toward maturation and spawning followed by the reverse process once spawning starts. This process can be quantified in mounted transverse sections through the same approximate part of the oyster's body by measuring the gonad and total body areas. Combined with stereological volumetric measurements (gonad volume fraction) to account for gamete density, these measurements represent a precise and direct method for comparison of the relative reproductive development among populations of oysters from different locations and in different years.

Difficulties in application of the technique and adequate solutions to them are illustrated using transverse sections of oysters collected from the James River, Virginia, in 1984 and in the 1960's.

IMPORTANCE OF TRIACYLGLYCERIDES AS A FATTY ACID RESERVE IN LARVAE OF THE EUROPEAN OYSTER *OSTREA EDULIS*

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The fatty acid profiles in all of the acyl-lipid classes of 1-day and 10-day old larvae of European oyster *Ostrea edulis* (L.) were studied in detail by capillary gas-liquid chromatography.

No significant changes in the fatty acids were detected between the different larval stages.

Total lipid fatty acids showed a higher degree of unsaturation than previously reported. This may be a consequence of the extraction of lipids from the living tissues without sample storage.

One third of the triacylglyceride fatty acids were polyunsaturated. In agreement with the quantitative importance of triacylglycerides in bivalve larvae, it is suggested that this lipid fraction may act as a temporary reservoir of physiologically important polyunsaturated fatty acids. Free fatty acids and fatty acids from the minor lipid classes will be discussed in terms of their possible origin and physiological significances.

THE EFFECT OF AN ALGAL BLOOM ISOLATE ON THE GROWTH AND SURVIVAL OF BAY SCALLOP (*ARGOPECTEN IRRADIANS*) LARVAE

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Recurring algal blooms have been implicated in the recent devastation of bay scallop (*Argopecten irradians*) populations in the coastal bays of eastern Long Island, New York. *Minutocellus polymorpha*, a centric diatom present in these blooms, was isolated from a field sample of Little Peconic Bay water taken in July, 1985 during the height of that year's bloom. Growth is shell length and the survival of bay scallop larvae were determined as the larvae were fed the bloom isolate and *Isochrysis* sp., Tahitian strain (T. *Iso.*), each at two concentrations corresponding in algal cell volume to optimal and bloom concentrations. Clearance rates for both algal species were measured through the completion of larval metamorphosis. Absorption efficiency was determined for both species of algae using a dual radiotracer method in which algae were labeled with both ^{51}Cr and ^{14}C.

The survival of the larvae was not significantly affected by different treatments of algae. Growth coefficients for scallop larvae fed the bloom isolate were lower than those fed T. *Iso.* Larvae also absorbed less carbon from the bloom isolate than from T. *Iso.* On a cell volume basis, clearance rates for the bloom isolate were comparable with those measured for T. *Iso.* until after completion of metamorphosis when T. *Iso.* began to be cleared at a greater rate than *M. polymorpha*.

DEVELOPMENT OF A MODEL TO SEED MUSSEL (*MYTILUS EDULIS*) BOTTOM LEASES TO THEIR CARRYING CAPACITY

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Select wild seed of *Mytilus edulis* was planted on three mussel bottom leases in Maine and observations were made on density-dependent growth and the depletion of food particles over a series of tidal cycles. Mussels sampled from the edge and middle of

bottom patches over three meters in diameter showed significant differences in growth rates in terms of shell length, dry meat weight and average shell volume. A 40% reduction in growth rate in the middle of the large patches was accompanied by reductions in food particle densities above the mussels at low current speeds. The results of these experiments are discussed in light of current theories on the depletion of seston in the benthic boundary layer, and the development of a carrying capacity model for each grow-out site.

RESPONSE TO SELECTION FOR GROWTH IN *OSTREA EDULIS:* SECOND GENERATION

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In 1980 lines of the European oyster, *Ostrea edulis*, selected for live weight were produced including high and low first generation selected lines and high selected second generation lines. Unselected control lines were produced from both the stock from which the selected lines were derived and from a recently imported stock. The lines were replicated in 2 sets. The means of the lines after 3 growing seasons showed a response to selection over the 2 generations in spite of the inbreeding which had previously been demonstrated in the stock. The unselected lines of the recently imported stock were about 25% heavier than the second generation selected lines. These results underscore the importance of evaluating and utilizing stock differences in aquaculture breeding programs. The selection program for improved oysters for culture in Nova Scotia is continuing with this new stock. Crosses with the old selected stock have also been done to incorporate the selected genes into a synthetic stock.

SPERM TRANSFER IN THE BROODING BIVALVE *OSTREA EDULIS*

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Ostrea species are well known to spawn their sperm as morulae or "balls," each containing thousands of cells. I have examined the ultrastructure of the morulae, distribution of cell surface sugar moieties, kinetics of morula breakdown in normal and modified seawater to investigate the mechanism of sperm transfer in *O. edulis*.

The morulae are composed of a central core of vesicles, formed by the extraneous cell membranes produced during spermatid condensation. Sperm heads are embedded in this core and the whole structure is held intact by a distinct extracellular matrix (ECM). Flagella appear to lack this ECM and a variety of FITC-conjugated lectins that stain the vesicular core and sperm heads do not stain the flagella.

After release into seawater, the sperm flagella activate and individual sperm cells are gradually released over a number of hours, coinciding with the dissolution of the ECM. Morula breakdown is enhanced by high pH seawater and non-cytolytic concentrations of butanol, which indicate that the adhesion factor is a peripherally-associated membrane component.

These findings are discussed in the context of other methods of bulk sperm transfer found in brooding bivalves and their potential relevance to applied research.

EFFECT OF EXOGENOUS FACTORS ON MOLTING OF JUVENILE BLUE CRABS *CALLINECTES SAPIDUS*

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In single treatment studies utilizing individually held juvenile blue crabs, the intermolt duration was least for the following holding conditions: container size of 3 inches, clear containers, presence of a substrate, water replenishment every second day, and morning water changes and evening feeding. The significance and experimental details from 25 studies conducted over a 3-year period are presented.

SURVIVAL OF *PENAEUS VANNAMEI* POSTLARVAE CHALLENGED WITH LOW-SALINITY WATER

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Penaeus vannamei 8- and 22-day-old postlarvae produced at three different hatcheries with broodstock from two different countries were obtained on seven different occasions over a three-year period. Ten replicates containing 10 animals each were challenged at five salinities for 24 and 120 hours. Overall survival of 22-day-old postlarvae transferred directly from 32-parts per thousand (ppt) water to waters of 32 ppt, 16 ppt, 8 ppt, 4 ppt, and 2 ppt were 89.8%, 92.0%, 75.8%, 52.6%, and 21.0%, respectively. Survival of postlarvae was better for 22-day-old larvae than 8-day-old larvae, and survival of postlarvae was less at 5-day ex-

posure than 1-day exposure. Survival of postlarvae varied gently for different groups of larvae.

THE MOULT CYCLE OF MALE SNOW CRAB (*CHIONOECETES OPILIO*) IN CAPTIVITY: EVIDENCE FOR A TERMINAL MOULT AT MATURITY AND THE EFFECTS OF STARVATION AND EYESTALK ABLATION

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Sixty-eight male snow crabs, 67–94 mm carapace width, were held in the laboratory for 12–15 months to investigate moulting. Changes in shell rigidity and colour, the ecdysial suture, setal development, and feeding behaviour provided useful criteria for defining the moult cycle of this species.

Thirty-four of the crabs were bilaterally eyestalk ablated and half of these (17) and half (17) of the intact crabs were starved for 6 months. The remaining 17 ablated crabs and 17 intact crabs were fed twice weekly. Morphometric maturity and gonad weight and condition were assessed.

All the morphometrically immature crabs (15) entered premoult and 8 moulted. However, none of the 53 mature crabs moulted or progressed into premoult. These data provide evidence for a terminal moult at maturity in male snow crabs. Starvation delayed entry into premoult and prevented progress into later premoult stages and moult in 75% of the crabs that entered premoult. Bilateral eyestalk ablation did not result in early entry into premoult, acceleration of the premoult period, or early moulting. All the ablated crabs died at moult. The fed immature crabs entered premoult between mid-December and mid-January and moulting occurred over an 8-week period between mid-February and mid-April.

Implications of our findings to commercial fisheries for *Chionoecetes* spp. worldwide are discussed.

GROWTH RATES OF *HOMARUS AMERICANUS* FROM OFFSHORE AREAS OF THE SCOTIAN SHELF, AND THE EFFECT OF THE INTERMOLT PERIOD ON POPULATION SIZE STRUCTURE

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Molt increment and intermolt period obtained through tagging studies are presented for lobsters (*Homarus americanus*) from the offshore regions of the Scotian Shelf. Growth data are presented for lobsters ranging from 70 mm to 180 mm carapace length, and growth rates are compared with results of other studies within the Gulf of Maine Area. Population size-frequency distributions are simulated from growth data, and the importance of the intermolt period in determining the population size structure is discussed with reference to the spatial variation in size frequencies in the commercial catch.

HARD CLAM RECRUITMENT IN LONG ISLAND SOUND: A LIFE-HISTORY APPROACH

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A study of the biological and physical processes that influence recruitment of the hard clam, *Mercenaria mercenaria*, was begun in 1986. The overall goal of the multi-year study is to identify the life-history stages of the hard clam that most critically limit natural production. Experiments in 1986 were designed to determine whether larval settlement occurred at specific sites around the perimeter of Long Island Sound, and the relative growth rate of clams at those sites. Stations were located at the 5 m depth contour, were out of the influence of major riverine inputs or polluted harbors, and were chosen to be relatively uniform in substrate type. Settlement was monitored in 21 cm × 21 cm × 5 cm plastic boxes, filled with either natural substrate from the site or with a standard sand and covered with 8 mm plastic mesh. Growth of 10 mm hatchery-reared clams was determined by measuring groups held at a density of 500/m^2 in 0.4 m^2 plastic-coated wire mesh cages with 8 mm openings. The cages were buried approximately 10 cm into the substrate. Divers were used for all gear deployment and subsequent sampling.

Mercenaria settlement occurred at all stations, and site differences are discussed. Seasonal growth of planted clams was statis-

tically different at the four Connecticut stations for which complete growth data were obtained. Growth of the clams did not simply reflect known east-west gradients of salinity, temperature, phytoplankton abundance or pollutant levels. Based on 1986 results, three sites that produced very different growth results were chosen for further study in 1987. The new experimental emphasis will be on density-dependent growth at the sites. It will include measurements of food flux that may be critical to clam production. Settlement will be monitored on a more frequent basis in order to separate settlement success from post-settlement mortality.

MECHANIZED SEED HARVESTING OF *MYA ARENARIA*

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Two mechanized systems have been developed for the collection of ½"–1" *Mya arenaria* seed, a lightweight, portable unit for use on intertidal flats and a catamaran-based machine for operation in water depths up to 10 ft. Both devices incorporate a cutting blade and water jets on a winch-propelled dredge designed to remove a thin layer of sediment from which the seed clams are then mechanically separated for transplanting to productive but dug-out flats.

Design, construction and testing of the machines are described, together with preliminary results from the first two years of operation. Information is presented on mortality rates of the harvested seed, the impact of the dredge on the flats, and the potential applications for this concept in Maine's clam management program.

ESTIMATION OF GROWTH AND POPULATION SIZE OF THE FIGHTING CONCH, *STROMBUS PUGILIS*, WITH A COMPARISON OF THE FABENS AND ELEFAN METHODS FOR ESTIMATING VON BERTALANFFY GROWTH PARAMETERS

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Growth, population size and seasonality were estimated for *Strombus pugilis* living in a shallow mangrove surrounded bay on the south coast of Puerto Rico. A total of 847 conch were tagged during 22 months. Sampling occurred every 60 days and was conducted by swimming transects in an area of roughly 100 m^2. Siphonal length, lip thickness and weight were measured, and sex determined during each mark-recapture event. Changes in population size, estimated by the Jolly-Seber model, correlated with changes in mean temperature.

Changes in adult lip thickness were found to be the best estimator of growth and age. Only 1% of the recaptured conch were juvenile. Faben's and Pauly's ELEFAN methods were used to estimate Von Bertalanffy growth parameters. The former uses mark-recapture data, the latter uses primarily size frequently data, but can also incorporate up to 100 mark-recapture measurements. Both growth curves developed were plotted on lip-thickness-frequency distributions and compared with shifts in the peaks. Fabens' model gave an L_∞ = of 5.82 mm and a k of 0.904; the ELEFAN model gave an L_∞ = of 8.55 mm and a k of 0.703. Addition of 100 mark-recapture values to the ELEFAN data resulted in only a small change in L_∞ and k (8.35 mm; 0.830). Although seasonality was not apparent from the ELEFAN method, tagging observations show highest growth during September through November and lowest during November through January, corresponding to the periods of highest and lowest temperature, respectively. Differences between the methods to estimate growth are discussed.

FIRST YEAR GROWTH OF TWO DIVERSE POPULATIONS OF AMERICAN OYSTERS *CRASSOSTREA VIRGINICA* (GMELIN) AND THEIR RECIPROCAL CROSSES

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The Maine Agricultural Experiment Station has embarked on a long-term program to improve growth rate in the American oyster by evaluating various pure-line and cross-line combinations at three temperature diverse sites in the Damariscotta (ME) River estuary. Peak 1986 mid-summer temperatures ranged from 22 to 24°C and 17 to 19°C at the upper and lower sites respectively. Results from initial matings between two diverse populations and their reciprocal crosses are reported. Stocks utilized were a commercial non-selected fine (F) from Long Island Sound and animals from the MSX resistant stock (D) of Haskin and Ford. Pure line offspring from F × F and D × D were compared to one another

and to offspring from F♂ x D♀ and D♂ × F♀. All animals were spawned in April 1986 and placed at the three estuarine sites in June.

At seven months of age significant differences were seen between growth rates of the pure lines with F × F animals being significantly larger at all sites. The D × D animals were significantly smaller than either of the reciprocal crosses while F × F animals were never significantly different from the two crosses. The two cross-line combinations were generally not significantly different from one another. The combined performance of the pure line animals versus the crosses showed the latter to be consistently larger but the differences were never statistically significant. There was a significant site effect with animals being larger in the warmer, less saline sites.

PARALYTIC SHELLFISH POISONING IN MAINE: MONITORING A MONSTER

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The historical presence of the toxic dinoflagellate, *Protogonyaulax tamarensis*, and its role in paralytic shellfish poisoning (PSP) in the Gulf of Maine is reviewed. This continued threat to public health has resulted in the development of a comprehensive monitoring program designed to maximize the safe harvest of uncontaminated shellfish. This system is described in detail. The increased levels of human consumption of shellfish in Maine, the increased intensity of fishing effort for species such as *Arctica islandica*, the increased efforts to culture *Mytilus edulis* and the efforts to establish a market for whole scallops (*Placopecten magellanicus*) have all necessitated modifications to the monitoring system and these are described. Data are presented for PSP distribution and concentrations from 1980–1986. The success of the monitoring program and the possible presence of other toxic algal species in the Gulf of Maine will be discussed.

COMPARATIVE STUDY OF OXYGEN UPTAKE RATES IN INDIVIDUAL LARVAE AND POSTLARVAE OF THE BAY SCALLOP, *ARGOPECTEN IRRADIANS*

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Standard methods for gradient-diver microrespirometry were modified to determine oxygen uptake for individual larvae and postlarvae of the bay scallop, *Argopecten irradians*. Gradient-diver methods are particularly useful for work with molluscan larvae: they are very sensitive and do not require the culture medium to be stirred. Measurement of respiration rates of individual larvae makes it possible to estimate individual variability in oxygen uptake, to estimate relationships between specific behaviors and respiration, and to improve the accuracy of rate estimates by eliminating larval interactions which occur when many larvae are enclosed in a respirometer chamber. "Fishpole" microbalances (3–12 μm quartz fibers which are deflected by the weight of larvae placed on them) were fabricated, calibrated and used to measure dry weight of individual larvae over the range of 0.1–50 μg. Cumulative and weight-specific oxygen uptake rates were analyzed as a function of larval size, age, development from onset to completion of metamorphosis, activity level and source of larvae. Quantitative recovery of the alkaline absorbent used in each diver was not possible thus preventing the calculation of respiratory quotients based on measurements of CO_2 in the absorbent.

As expected, oxygen uptake increased with larval size in all experiments while weight-specific oxygen uptake decreased with size. Source of larvae and activity level significantly affected overall uptake rates which ranged from $4.6–15.2 \times 10^{-3}$ μl $O_2 \cdot hr^{-1} \cdot \mu g^{-1}$. Results are in close agreement with uptake rates reported for other molluscan larvae. Significant differences in weight-specific oxygen uptake rates were found between laboratory-reared and wild-caught larvae and between offspring of Long Island and Connecticut scallops.

DOES LECTIN FROM THE DIGESTIVE GLAND OF *PLACOPECTEN MAGELLANICUS* AID FILTER FEEDING?

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A lectin was purified from the digestive gland of *Placopecten magellanicus* by conventional protein purification methods and by affinity chromatography. Binding studies indicate that the lectin recognizes material containing polymeric *D*-3-deoxy-*manno*-octulopyranosonic acid or *N*-acetyl neuraminic acid providing these sugars are α-linked. The lectin agglutinates both picoplankton and phytoplankton and both plankton types test positively for the above sugars. The presence of appreciable quantities of these sugars in phytoplankton is surprising and the implications of this observation will be discussed.

The location of the lectin in the digestive gland suggests a role for this lectin in feeding. This was evaluated by feeding scallops a Gram-negative bacterium, a Gram-positive bacterium, and picoplankton while measuring uptake rates and lectin content. The lectin titer of scallops from the Eastern Shore of Nova Scotia was much higher than in scallops from the Bay of Fundy or Georges Bank. The implications of these findings will be discussed and a possible role for the lectin in the feeding mechanism of scallops is suggested.

LARVAL BEHAVIOUR OF THE SEA SCALLOP *PLACOPECTEN MAGELLANICUS* UNDER LABORATORY CONDITIONS: EFFECT OF LIGHT ON SWIMMING BEHAVIOUR THROUGHOUT DEVELOPMENT

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Larvae of *Placopecten magellanicus* were studied under culture conditions at 14°C to determine the effect of continuous light exposure on larval development and swimming behaviour. Every 2 or 3 days, a mixed diet consisting of *Chaetoceros gracilis*, *Chaetoceros calcitrans*, and *Isochrysis galbana* T-iso was added to the larvae beginning at age 4 days to age 30 days. Larval distribution, swimming paths, swimming speeds, and Reynolds numbers were analysed for larvae at 4, 6, 10, 16, 22, and 30 days after fertilization.

Changes in swimming behaviour were observed as the larvae grew older. They avoided the light and displayed a positive geotactism. Swimming speeds and larval distribution also changed throughout larval development. These observations were consistent with morphological and physiological changes, such as almost four-fold increases in dry tissue weight (including the shell), presence of the eyespot, and gill and foot development.

OBSERVATION ON SOME LIFE HISTORY ASPECTS OF A COMMERCIALLY EXPLOITED POPULATION OF *BUSYCON CANALICULATUM* (LINNE) IN NARRAGANSETT BAY, RHODE ISLAND

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Studies were conducted to determine movements, age structure, growth, population size, gonad development, and sex ratio for the whelk population.

Movement of marked whelks was random and not correlated with other variables such as growth or month. Most animals were recaptured within 286–917 meters of release point, but some others had moved 4587 meters.

Population age structure was determined using growth layers on the shell and growth rings on the operculum. Areas sampled displayed no discreet population segment. The dominant population constituent had 4–5 growth layers and a width of 141–210 millimeters (mm). A formula was developed by express estimated age.

Estimated Age = 0.76 (width in mm) + 0.07 (Wt. in Grams) − 36.65.

Average growth for all returned tagged animals was 2.6 mm regardless of time from release to recapture. ANOVA for growth over time is poorly correlated probably due to the noticeable chipping of the shell margin.

In areas of Narragansett Bay where the fishery is conducted, the population density is between 11,110 and 18,182 whelks per square kilometer (km^2) and the average biomass for the area was between 2389 and 3909 kilograms per km^2. It was also estimated that the annual survival rate is 65.8% and the annual mortality is 34.2%. Annual fishing mortality was determined to be 16.2%.

A subjective gonad index was used to judge sexual development of conchs. Shell width of animals with a well developed gonad = 58 mm. Below this size, the gonad development decreases to where there is no visible development at a shell size of 40–42 mm and below.

Approximately 31% of the population of *B. canaliculatum* in Narragansett Bay are males, and animals greater than 80 mm appear to be all females, while those animals less than 70 mm are approximately 59% males, and 50% females.

STANDARDIZATION OF DUNGENESS CRAB (*CANCER MAGISTER*) ABUNDANCE AND SIZE DISTRIBUTION WITHIN COMMERCIAL TRAPS BY DYNAMICALLY CORRECTING FOR THE EFFECTS OF SOAK TIME AND SELECTIVITY

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The catch rate of Dungeness crabs (*Cancer magister*) by commercial traps decreases over time due to changes in bait effectiveness and the tendency for crabs within traps to inhibit the entry of

more crabs. The results of two experiments to measure the effects of soak time and bait effectiveness, respectively, were analysed dynamically and simultaneously to estimate the size frequency distribution of crabs encountering a trap, and the parameters for models describing changes in bait effectiveness and agonistic behavior over time. This analysis also incorporated information from a third experiment which determined the probabilities of crabs of different sizes being retained by a trap.

Using these parameter estimates, commercial samples with different soak times may be standardized to a "virtual entry rate" for a soak time of zero, before the trap contents are modified by the above mentioned factors. This procedure proved useful for estimating the degree of exploitation of the Dungeness crab population near Tofino, B.C.

POPULATION GENETIC ANALYSIS OF THE QUEEN CONCH, *STROMBUS GIGAS*, IN BELIZE, CENTRAL AMERICA

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Natural populations of queen conch, *Strombus gigas*, were sampled and analyzed using protein electrophoretic techniques to determine the kind, extent and distribution of genetic variation among Belizean conch populations. The objective of these analyses was to determine whether single or multiple stocks of conch exist within Belizean waters. Sampling sites were selected to evaluate the influence of potential geographic, environmental and morphological stock isolating mechanisms. All sites were sampled in either 1985 or 1986 and several sites were sampled in both years.

Six enzyme loci were shown to be resolvable and polymorphic in the Belizean conch populations. Significant genetic differences were found to exist among Belizean conch populations. Local populations show significantly non-homogeneous frequency distributions at two of the six polymorphic loci studied. Those populations sampled in consecutive years showed similar allele frequencies confirming that the methods employed provided reliable estimates of allele frequencies and consequently that the observed differences were real. However, the differences do not appear to be patterned with respect to potential stock isolating mechanisms. Evidence against local stock differentiation is presented and alternative explanations of the observed patterns of variation are discussed.

GROWTH AND MORTALITY OF *MYTILUS EDULIS* IN THE COASTAL WATERS OF BRITISH COLUMBIA

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Subtidal populations of the blue mussel, *Mytilus edulis*, were studied at 3 sites in the coastal waters surrounding Vancouver Island, British Columbia. A reciprocal transplant experiment was conducted to investigate the influence of both the environment (grow-out site) and potential genetic differences among *M. edulis* populations (seed source) on mortality and growth. Mussels 25–45 mm in length were collected from each site and transported to the other 2 sites where they were grown alongside mussels from the endemic population. Groups of mussels attached to strips of plastic mesh were suspended from rafts or longlines and sampled at 6 week intervals from April to October, 1986. Individually tagged mussels were measured repeatedly to determine rates of growth.

Results of 2-factor ANOVA showed that both grow-out site and seed source had significant effects on survival. Mussels grown at the northern site had the highest rate of survival while the mussel seed that survived best was collected from the west coast site. Highest mortality rates occurred in the latter half of the summer. There was no strong evidence that mortality was size dependent.

Grow-out site and seed source also had significant effects on growth rates. Seed mussels collected from both the west coast and northern sites grew equally well at those 2 sites while growth rates were lowest for all mussels at the east coast site in the Strait of Georgia. Growth rates were highest in the spring and early summer and were very low in the late summer.

CHARACTERISTICS OF GLYCOGEN SYNTHASE ACTIVITY IN THE DIGESTIVE DIVERTICULA OF THE OYSTER, *CRASSOSTREA VIRGINICA* GMELIN

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In bivalve molluscs, glycogen metabolism is keyed to the reproductive cycle and also sustains the animals during periods of starvation and anoxia. In mammals glycogenesis is regulated in part by control of the activity of glycogen synthase (*GS*). Only a few studies of this enzyme have been made in molluscs.

GS activity has been found in the digestive diverticula of the oyster. The enzyme exists in two forms, *GSI* and *GSD*. In oysters held unfed in the laboratory for 25 days, the percentage of *GSI* activity increased. *GSD* was purified 1600 fold. The $K_{M(UDPG)}$ was found to be 1.1 mM; $K_{a(G6P)}$ was 5.0 mM. Enzymatic activity was unaffected by 10 mM ADP and AMP, but 10 mM ATP, cAMP and orthophosphate caused 12, 14, and 53 percent inhibition, respectively. Addition of glucose to homogenates of digestive diverticula caused GSI activity to increase. The elevation in GSI was apparent within 10 min. and was maintained for at least 45 min.

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RELATIVE IMPORTANCE OF PHYTOPLANKTON AND ORGANIC DETRITUS AS FOOD SOURCES FOR THE SUSPENSION-FEEDING BIVALVE, *MYTILUS EDULIS*, IN LONG ISLAND

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Our study was designed to determine the absorption efficiencies of two different types of food sources, phytoplankton and organic detritus, by the blue mussel *Mytilus edulis* throughout the year. Water from the surface and 1 m above the bottom was collected monthly beginning in November, 1986 at a 20 m^2 site in Long Island Sound. Dual-radiotracer methods were employed to label phytoplankton (C-14 bicarbonate and Cr-51) and organic detritus (C-14 formaldehyde and Cr-51). Absorption efficiencies were estimated by comparing the ratio of Cr-51:C-14 ingested to that of feces. Analyses of total seston concentration, chlorophyll a, phaeophytin, particulate organic carbon and nitrogen, and bacterial enumeration were conducted. Changes in phytoplankton species assemblages were also investigated.

The results to date demonstrated that absorption efficiencies of phytoplankton were significantly higher than those of organic detritus in winter and spring for both surface and bottom water. Organic detritus collected in winter was utilized with lower efficiencies than that collected in spring. Further results will be presented with a discussion of seasonal differences of the food sources.

ON THE IMPORTANCE OF PHOTOSYNTHETIC PICOPLANKTON IN THE NUTRITION OF BIVALVE MOLLUSCS, WITH SPECIFIC REFERENCE TO THE SUMMER 1985 NARRAGANSETT BAY "BROWN TIDE" AND ASSOCIATED MASS MORTALITIES IN BLUE MUSSEL (*MYTILUS EDULIS*) POPULATIONS

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Picoplankton are bacterial-sized cells in the 0.2 to 2.0 μm diameter size fraction of the plankton. In coastal waters their abundance is typically 10^6 cells/1 ml^{-1}, consisting mainly of photosynthetic cyanobacteria (5×10^5 cells/ml^{-1}) but also eucaryotic cells in excess of 10^3 cells/ml^{-1}. The diversity of forms within these groups has only been explored through transmission electron microscopy techniques during the last decade. The possible importance of picoplankton in the nutrition of bivalves has been overlooked because of low retention efficiency and non-digestability of these cells. Recent field studies, however, have demonstrated both beneficial and detrimental effects of picoplankton on the nutrition of bivalves. In Narragansett Bay, massive mortalities among blue mussel (*Mytilus edulis*) populations were observed in conjunction with an extremely dense picoalgal bloom. The dominant alga, being greater than 10^6 cells/ml^{-1} and 95% by numerical abundance, previously was unknown to these waters. Feeding experiments demonstrated anorexigenic properties of the bloom algae on bivalve molluscs, whereas similar effects were not observed with other similarly-sized algae isolated from the bloom. This event demonstrates the great potential of the picoplankton and its species composition to influence nutrition of bivalve molluscs.

THE VERTICAL DISTRIBUTION OF SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*) LARVAE IN THE BAY OF FUNDY AND ON GEORGES BANK

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Sea scallop larvae were collected from discrete depth intervals using a high-volume (400 litres per minute) pump during the autumns of 1984 to 1986. The number of depth profiles completed at any one station ranged from one to 25 (a 50-hour anchor station).

In both the Bay of Fundy and on Georges Bank, the degree to which scallop larvae were aggregated at any depth was related to the extent to which the water column was stratified. At stations where a moderate thermocline was present [temperature change of approximately 1°C in 10 to 15 meters (m)], pronounced peaks in larval concentration were associated with the thermocline. In well-mixed areas, larvae tended to be distributed equally throughout the water column.

A diurnal vertical migration of sea scallop larvae can be inferred from day-night differences at the 50-hour station. Weighted mean depth of larvae there ranged from 5.1 to 11.5 m during the day (0830–2030 hours) and from 4.0 to 6.8 m during the night.

Differences in vertical distribution related to larval size were evident at some stations, but the patterns were not consistent. There is some evidence that the largest larvae (greater than 250 microns) occupy a greater range of depths.

MAINTENANCE OF HETEROZYGOSITY IN OYSTERS DURING SELECTIVE BREEDING FOR TOLERANCE TO MSX INFECTIONS

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Hatchery-reared strains of oysters, *Crassostrea virginica*, have been selected for resistance to *Haplosporidium nelsoni* (MSX). Pedigrees were kept for five strains that were in their fifth and six generations of inbreeding. We determined the genetically effective number of parents in each generation and estimated the inbreeding coefficient for each strain. This coefficient was used to predict the current level of heterozygosity of each strain.

The inbred strains, and samples of wild populations from which they derived, were assayed electrophoretically for variation at the *Ap*, *Lap-1*, *Lap-2*, *Aat-2*, *Pgi*, and *Pgm* loci. Mean heterozygosity of the inbred strains was not significantly less than that of the wild oysters. At nearly all loci, rare alleles were lost in the inbred strains, and in a few cases individual loci had become fixed, but overall, heterozygosity had not declined significantly. Genic heterozygosity is affected by both the richness of alleles and the evenness of allelic frequencies. In all five strains, allelic richness declined as expected under the inbreeding model, but for many loci, allelic evenness increased, preserving the high heterozygosity levels.

DISTRIBUTION, ABUNDANCE AND SPECIES RATIO OF WHELKS (*BUSYCON* SP.) IN NEW JERSEY COASTAL WATERS

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Whelk abundance was assessed during hydraulic dredge surveys of the surf clam (*Spisula solidissima*) resource in the inshore (0–5.5 km from shore) waters off the New Jersey coast from 1973 to 1985. Surveys were conducted between May and September. Sample frequency approximated one station per square nautical mile (3.4 square kilometers). Number of each species per standard tow, water depth, and latitude were determined for all stations occupied in 1984 (n = 296).

Whelk species collected (in order of decreasing abundance) were: *Busycon carica*, *B. canaliculatum* and (rarely) *B. contrarium*. Frequency of occurrence and abundance for all species were higher off the southern half of the state. No correlation was found between species abundance and sediment type (measured as median grain size) or depth. Estimated stock size and potential for a commercial fishery are discussed.

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USE OF SPECIFIC BACTERIAL BIOFILMS AND THEIR PRODUCTS TO ENHANCE SPAT SET OF THE OYSTERS *CRASSOSTREA VIRGINICA* AND *C. GIGAS*

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We have demonstrated that specific marine bacteria synthesize chemical cues for search/crawl behavior in larvae of the oysters *Crassostrea virginica* and *C. gigas*. LST, a new, melanin-producing species of *Alteromonas* isolated from oyster setting tanks, is particularly active in inducing larval behavior. Enzyme assays and fractionation of bacterial products indicate that, in the case of LST, the enzyme involved in melanin production, tyrosinase, also mediates the synthesis of larval behavior inducers. Evidence suggests that these compounds are closely related to L-dihydroxyphenylalanine (L-DOPA), an intermediate in the production of melanin. LST also excretes an adhesive polysaccharide that appears to condition surfaces for cementation and metamorphosis of oyster larvae.

We have conducted experiments to evaluate the ability of L-DOPA, of bacterial films, and of purified bacterial inducers and polysaccharides to enhance the setting and survival of *C. virginica* in Maryland oyster hatcheries. Biofilms of LST led to a 2- to 3-fold increase in spat set on various types of surfaces. Manipulation of biofilm growth conditions indicated that both tyrosinase products and exopolysaccharides are important *in situ* determinants of settlement and metamorphosis in *C. virginica* and *C. gigas*.

INTERTIDAL POPULATIONS OF FOUR SPECIES OF WHELKS (*BUSYCON*) IN WASSAW SOUND, GEORGIA

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Four species of *Busycon* occur in the coastal waters of Georgia: the Knobbed Whelk, *B. carica*, and the Lightning Whelk, *B. contrarium*, in intertidal to subtidal areas; the Channeled Whelk, *B. canaliculatum*, occasionally intertidally, but primarily subtidally; and the Pear Whelk, *B. spiratum*, subtidally. Because oysters, *Crassostrea virginica*, and hard clams, *Mercenaria mercenaria*, occur intertidally in Georgia and intertidal whelks prey upon these commercially important shellfish, the abundance, migrational and feeding patterns of intertidal whelks were studied.

At the mouth of the Wassaw Sound, Georgia (a high saline area), *B. carica* accounted for 79%, *B. contrarium* 21% and *B. canaliculatum* less than 1% of the total number (N = 1191) of whelks sampled. *B. carica* migrates higher up into the intertidal zone than does *B. contrarium*. *B. canaliculatum* only occurs intertidally on low spring tides. Whelks migrate seasonally onto and off intertidal flats where oysters and clams occur. Densities are highest in fall and spring and lowest in winter and summer. A low percentage (8%) of whelks was found actively feeding. Of these, 54% were consuming *Mercenaria mercenaria* and 46% were consuming *Crassostrea virginica*.

Of 195 whelks sexed, female *B. carica* outnumbered males 11 to 1 and were larger in shell length (14.8 ± 3.3 cm) than males (10.9 ± 2.8 cm). No males were found among the 57 *B. contrarium* sampled.

SIZE DISTRIBUTION OF V-NOTCHED LOBSTERS (*HOMARUS AMERICANUS*) ALONG THE MAINE COAST

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As a means of conserving a proportion of the lobster brood stock, Maine lobstermen voluntarily mark egged lobsters with a V-notch cut in the right uropod. These lobsters are protected and cannot be landed in Maine.

Fifteen lobstermen in four areas along the Maine coast recorded carapace lengths of V-notched and egged lobsters in their trap catch over three ten day periods, in early June, late July–early August, and late September–early October. Lobsters were categorized as: V-notched with eggs, V-notched without eggs, and non-V-notched with eggs. Measured lobsters were marked with a blue band on the claw, and the number of recaptures was recorded. Researchers accompanied fishermen and measured lobsters on thirteen days during the survey.

Mean carapace lengths of V-notched lobsters and egged lobsters were 95.10 ± 0.14 mm and 104.38 ± 0.35 mm, respectively. V-notched lobsters were significantly ($P < 0.01$) smaller than egged lobsters. Lobsters caught in the southern areas were significantly smaller than those caught farther north. Seventeen percent of V-notched lobsters carried eggs, and seventy percent of egged females were V-notched. Eleven percent of marked V-notched lobsters were recaptured. No significant difference was detected between data recorded by fishermen and by researchers.

Because the number of eggs a lobster will carry increases geometrically with size, the results indicate that the V-notch lobster contribution to egg production is far more significant than previously predicted on the basis of numbers of V-notched lobsters alone.

AN AUTOMATED CONTINUOUS MASS CULTURE SYSTEM FOR MICROALGAE

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We have designed, built, and tested an automated continuous mass culture system based on the cage culture turbidostat. The system allowed the continuous growth of diatoms at rates greater than could be achieved in batch cultures. Manipulation of the growth conditions, particularly the supply of inorganic nitrogen, resulted in predictable changes in the biochemical composition of the organisms. Cultures kept at the optimum density of $2-2.2 \times 10^6$ cells/ml at a light level of 165 $\mu E/m^2$/day averaged 2 divisions/day, producing harvests of $1.3-2 \times 10^6$ cells/day as a sustainable yield, with the cells not senescent, but in log growth phase. It is possible that denser cultures could be held at this division rate with more light, or with light brought into the growth chamber with light pipes. We would suggest this form of phytoplankton culture as a substitute for either batch or semi-continuous culture of food organisms for larval shellfish.

EFFECTS OF MICROALGAL METABOLITES ON PARTICLE SELECTION AND FILTRATION RATES OF MUSSELS

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Evidence is presented which indicates that nontoxic microalgal ectocrines mediate the feeding behavior of the mussel *Mytilus edulis* (L.). Monoclonal cultures of three species of marine microalgae were grown in the laboratory on Guillard's f/2 media. Cells were removed from cultures by gentle filtration, leaving dissolved microalgal ectocrines in culture filtrates. These filtrates were then used to determine effects of adsorbed epi-particulate ectocrines on the particle selection of mussels and to determine effects of dissolved ectocrines on the filtration rate of mussel.

Ectocrines were adsorbed onto either reverse phase (lipophilic) or normal phase (hydrophilic) microparticles (10.0 μ) and delivered to mussels with an equal concentration of particles treated with sea water and a nutrient control. Feces and pseudofeces were collected and proportion of treated and control beads were compared. Results indicated that mussels select microparticles treated with ectocrines over those treated with the control.

Dissolved ectocrines were delivered to mussels in a non-static flow-through apparatus and removal of polystyrene beads (4.0–5.0 μ) was used to determine filtration rates. Bioassay results showed that mussels exposed to dissolved ectocrines had significantly higher filtration rates than mussels exposed to sea water and a nutrient control.

This research provides evidence that pre-ingestive chemical cues from microalgae influence mussel feeding behavior. Further experiments are being conducted to fractionate culture filtrates and determine the chemical nature of stimulatory substances.

ESTIMATING BIVALVE CARRYING CAPACITY AND POTENTIAL PRODUCTION

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State-of-the-art methods for estimating carrying capacity and production of bivalves are considered. Hydrodynamic conditions involved include natural bottom or open channel flow, suspension culture and pipe flow. A modified Wildish and Kristmanson (1979) model is used which treats populations rather than individual bivalves. Biological phenomena of interest in the model include the "seston depletion effect," bivalve density and pumping capacity and the spatial extent of the bivalve bed.

The utility of the model is demonstrated with practical examples involving potential giant scallop, *Placopecten magellanicus*, culture in the Bay of Fundy, Canada.

HETEROZYGOTE SUPERIORITY AND GENETIC LOAD FOR GROWTH IN NATURAL POPULATIONS OF MARINE BIVALVES

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Several studies have demonstrated positive correlations between electrophoretic heterozygosity and growth or viability rates in marine bivalves. These correlations led to studies of the physiological basis of variation in growth rate among individuals. The emerging hypothesis is that faster growing individuals have lower energetic requirements for basal metabolism thus diverting a higher proportion of available energy to anabolic processes, such as growth and reproduction. Assuming this difference in allocation of energy deposits between slow and fast growing individuals

is real, we may ask 1) to what extent this is a genetically determined property, and 2) whether reduction of energy requirements for basal metabolism results from heterozygosity for allelic genes segregating in the population or from avoidance of homozygosity for deleterious genes that are introduced in the population by mutation. Critical examination of results from our and other laboratories supports the latter explanation of the heterozygosity growth correlation. Recent cytogenetic studies in oysters (Thiriot-Quievreux, *Genetica* 70:225–231, 1986) revealed high rates of incidence of chromosomal abnormalities, apparently resulting from errors during mitosis and meiosis. Thus, it is conceivable that the mutation-selection balance maintains a high level of genetic load in natural populations of marine bivalves. The implications of these observations for the exploitation of natural stocks or the domestication of these species will be discussed. Support by an NSERC operating grant.

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ABSTRACTS OF TECHNICAL PAPERS

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LARVAE AND RECRUITMENT

SWIMMING BEHAVIOUR OF MACTRID LARVAE IN RESPONSE TO SALINITY GRADIENTS

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Rangia cuneata, Mulinia lateralis and *Spisula solidissima* are three mactrid bivalves which are considered to be oligohaline, euryhaline and marine stenohaline, respectively. We posed the question: to what extent is adult distribution influenced by the ability of their respective larvae to depth regulate in response to salinity gradients? Larvae of *R. cuneata, M. lateralis* and *S. solidissima* were cultured at 10, 25 and 30 ppt, respectively. At three stages during development—straight hinge, umbo and pediveliger, larvae were exposed to salinity gradients or discontinuities formed by layering the salinity of origin with water of a second salinity that differed by 5, 10 or 15 ppt. Larvae were allowed to equilibrate in these treatments and their distribution relative to salinity recorded. All species exhibited tendencies to aggregate near the discontinuity; however, they also exhibited salinity preferences: *R. cuneata*, ≤ 10 ppt; *M. lateralis*, 20–30 ppt; *S. solidissima*, 25–30 ppt. Swimming speed at each salinity was also recorded. The results are discussed in relation to current understanding of estuarine circulation.

LARVAL *MERCENARIA* RECRUITMENT: LIFE IN MUDDY WATERS AND LITTLE AIR SUPPLY

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Recruitment of *Mercenaria* to benthic environments may require larvae to withstand hypoxic oxygen levels early in the morning, oxygen supersaturation as high as 11.5 mg l^{-1} (188%) in the afternoon, and suspended sediment loads exceeding 1000 mg l^{-1}. A rock tumblerlike device maintained particles in suspension during 48 h suspended sediment (0—2000 mg l^{-1}) and 24 h dissolved oxygen trials. Low dissolved oxygen experimental levels ranged from 1—6.5 mg l^{-1} (15–95%); supersaturated levels were 13.7—7.6 mg l^{-1} (180—95%) (ambient temperature differences cause discrepancy in correlation between mg l^{-1} and percent saturation). We determined that larval survival is not affected at any of the experimental treatments. However, growth was adversely affected by 2000 mg l^{-1} sediments and supersaturated oxygen. Events producing such levels may prolong larval stages, thereby increasing losses from predation and wastage.

DISCOCILIA AND PADDLE CILIA IN THE LARVAE OF *MULINIA LATERALIS* AND *SPISULA SOLIDISSIMA*

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The bivalve larval velum contains four bands of cilia: an inner and outer preoral band, an adoral and a postoral band. The preoral bands of compound cilia are generally considered to be used for both locomotion and food gathering. The adoral and postoral bands function in concert with the preoral bands in food gathering and transfer of food to the mouth. Cilia are usually described as cylindrical structures which taper to a blunt tip. Modified cilia with disc shaped (discocilia) or paddle shaped ends have been recorded in several invertebrate species. Here, for the first time, we demonstrate the presence of discocilia in the velum of *Mulinia lateralis* and paddle cilia in the velum of *Spisula solidissima*. Such cilia are restricted to the inner preoral bands and the central ciliary tuft. The presence of such cilia does not appear to increase the swimming velocity of these larvae in comparison to that of *Rangia cuneata* larvae of similar size. The possibility that these modified cilia have enhanced sensory capability remains to be tested.

INDUCTION OF SETTLEMENT AND METAMORPHOSIS OF *MYTILUS EDULIS* (L.) LARVAE BY DOPA-CONTAINING POLYPHENOLIC PROTEIN

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The purpose of the study was to determine the inductive potential of the Dopa-containing polyphenolic protein extracted from adult *M. edulis* feet. Experimental surfaces of plexiglass, glass, and nylon monofilament of three different diameters were coated using three different concentrations of protein.

A significant two to three fold induction of settlement and metamorphosis was observed on surfaces coated with polyphen-

olic protein, compared to the settlement and metamorphosis observed on control surfaces, and induction increased with increasing concentrations of protein. Consequently, these results are of particular importance when applied to aquaculture.

FACTORS AFFECTING SETTLEMENT OF THE AMERICAN OYSTER (*CRASSOSTREA VIRGINICA*) IN HIGH SALINITY SOUTHEASTERN ESTUARY

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Spat settlement patterns of the American oyster, *Crassostrea virginica*, were determined over a five year period using vertical arrays of collecting plates at three locations in the North Inlet Estuary, South Carolina. Biweekly collections indicated that setting began when average water temperatures reached 21.6° ± 0.7°C in April or May. The timing and duration of the settlement season was similar each year (April/May–October/November), with settlement being continuous and having two distinct peaks. However, the pattern of spatfall within years and overall abundance varied significantly from year to year. There were no consistent relationships between settlement intensity and late stage larval density in the water column, water temperature nor salinity. Although site differences in spat abundances were negligible, settlement varied significantly among horizontal and vertical positions within a site. In addition, comparisons between the tops and bottoms of spat collector plates after two week exposures indicated that differences between sides of collectors were not consistent among sites. These variations are attributed to both physical (aerial exposure, tidal current, sedimentation) and biological (predation, competition, gregariousness) factors. Additional short-term studies demonstrated how sampling frequency influences the interpretation of oyster spat settlement patterns.

USE OF IMAGE ANALYSIS IN DETERMINATION OF GROWTH AND MORTALITY RATES OF NEWLY SETTLED *CRASSOSTREA VIRGINICA*

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Image analysis techniques enabled the fate of individual oysters to be ascertained beginning from the initial hours of post-settlement life. Hatchery-reared larvae were allowed to settle on 25 cm^2 porcelain plates. The plates were magnified and photographed by a 35mm camera fitted with a 50mm macro lens and were then designated to various experimental treatments. Each plate was rephotographed over discrete time intervals during the experiment. The series of photographs thus attained were digitized onto a System 575 Digital Image Processing System. This computer system allowed the series of images to be sequentially displayed to produce a time-lapse progression, and individual oysters, as well as other sedentary organisms, could thus be identified through time. For each photograph in the time series, the sizes of the spat, expressed as areas, were determined by scaling the number of pixels composing each oyster to a known constant. From these measurements growth rates, calculated as the change in area (cm^2)/time interval, were determined. These methods, developed for an investigation into the effect of intertidal zonation on the growth and mortality of juvenile oysters, were found to be advantageous for both sampling and data processing. Image processing techniques are seen as a powerful tool for use in invertebrate research.

TEMPORAL AND SPATIAL PATTERNS OF RECRUITMENT OF *MERCENARIA* SPP. IN THE INDIAN RIVER LAGOON, FLORIDA

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Fifty stations were sampled quarterly in each of two shellfish bodies in the Indian River Lagoon from fall 1986 through summer 1987. Of the fifty stations, fifteen each were located randomly in east, middle, and west portions of areas open to harvest, and five were in areas closed to harvest. Depth and sedimentary characteristics were recorded at each station, and a 0.25 m^2 circular quadrat was worked into the substrate to a depth of approximately 10 cm. Quadrats were cleared of large clams by hand raking, and the top 5 cm of substrate were removed with a water powered, venturi driven suction dredge. Material removed was collected in a bag with 2 mm subcircular mesh. All *Mercenaria* spp. retained in the bag, as well as all clams raked, were preserved to be counted and measured for maximum shell length.

Average densities of recruits in the southern lagoon were 2.64, 4.72, 2.72, and 2.32/m^2 for fall, winter, spring, and summer. Recruitment was significantly higher during winter. Recruitment to areas closed to harvest was significantly higher than to open areas.

Recruitment in the northern lagoon was extremely low, averaging 0.16 recruits/m^2 across all dates and stations. Data were not sufficient to allow comparisons of areas within the northern lagoon, or between seasons.

MSX

EFFECTS OF THE PARASITE MSX *(HAPLOSPORIDIUM NELSONI)* ON THE BIOCHEMICAL COMPOSITION OF THE OYSTER, *CRASSOSTREA VIRGINICA*

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Tissue biochemical composition of oysters (*Crassostrea virginica*) from Delaware Bay was examined between May and November 1985 as a function of intensity of infection by the endoparasite *Haplosporidium nelsoni* (MSX). For each sample ($n = 30$) the lipid, glycogen, protein and ash content (mg DW) of a standard 100 mm oyster was determined for uninfected, epithelial and systemic infection categories. Only glycogen content varied seasonally, increasing from May to October after completion of the reproductive cycle. All biochemical components generally decreased in content with increasing MSX infection intensity (and duration). However, overall reductions were significantly different from uninfected oysters only in glycogen [epithelial ($P < 0.05$) and systemic ($P < 0.001$)], protein [systemic ($P < 0.05$)] and ash [systemic ($P < 0.02$)] categories. Thus glycogen is the substrate most readily catabolized to meet the energetic burden posed by MSX. The impairment by MSX of nutrient storage capability affects other metabolic functions such that the ecological fitness of surviving oysters is reduced.

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IMMUNOASSAY COMPARISON OF HAPLOSPORIDAN SPORES

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Haplosporidium spores infecting *Teredo navalis* have been described as morphologically indistinguishable from spores of *H. nelsoni* (MSX). To further test the hypothesis that these are the same parasite, immunoassay techniques were used to determine antigenic similarities or differences. Shipworms were collected in October 1987 from planks held six months at Wachapreague, Virginia. Sections of infected *Teredo* were placed in beakers of high salinity sea water which was changed daily until all tissue decayed. Spores were then sonicated to disperse clumps and fixed one hour in AFA. An emulsion of spores and Ribi adjuvant system was prepared for rabbit injection. Rabbit antibody to *Teredo* spores was tested by Immunogold Silver Staining against paraffin sections of *H. nelsoni* and *H. costalis* in *Crassostrea virginica*, *H. louisiana* in *Panopeus herbstii* and *Haplosporidium* sp. in *T. navalis*. Application of primary antibody was followed by affinity purified goat anti-rabbit IgG coated on 5 nm colloidal gold particles. The reaction was enhanced by precipitation of metallic silver; a positive reaction appeared as a dark brown to black signal at the site of each antigen-antibody complex. The only positive reaction to Rabbit anti-*Teredo* spore of the four haplosporidans tested occurred with infected *Teredo* tissue indicating that these spores are antigenically different from the others tested. These results suggest that *Haplosporidium* sp. from *Teredo navalis* is not *H. nelsoni*.

EXPERIMENTAL PLANTING OF SEED OYSTERS IN DELAWARE BAY PRODUCED FROM MSX RESISTANT STOCKS

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Since the summer of 1985, the oyster fishery in Delaware Bay has experienced widespread mortality of seed and commercial sized oysters due to a renewed outbreak of MSX. The combined effects of disease related mortality and poor natural production have had a near fatal impact on the oyster industry on both sides of the Bay.

The College of Marine Studies, Delaware Sea Grant Marine Advisory Service and Department of Natural Resources and Environmental Control have been working together since 1985 to evaluate the potential for transferring hatchery produced seed oysters

onto natural bottom in Delaware Bay. An additional objective was to compare the growth and survival of seed oysters produced from MSX resistant broodstock to wild stocks from Delaware Bay seed beds. With the cooperation of the Rutgers University Shellfish Laboratory, broodstock oysters with a high resistance to MSX (B × F) were used to produce approximately 1.5 million spat (20% inbred; 80% outcrossed). In October 1986, these seed oysters were planted on a 1 acre test plot in Delaware Bay. A similar number of naturally set 1986 year class oysters were moved to the site from the New Jersey seed beds and served as a control. Results from the first growing season (April—October 1987) are presented and discussed.

TOXINS

SMALL-SCALE SPATIAL HETEROGENEITY AND SEASONAL VARIATION IN THE QUANTITY AND COMPOSITION OF PARALYTIC SHELLFISH TOXINS RETAINED IN CHRONICALLY CONTAMINATED *MYA ARENARIA*

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The Baie des Capucins along the Gaspé coast of the lower St. Lawrence estuary was specifically selected as the study site due to the chronically high PSP toxin levels found throughout the year. In spite of posted warnings against the harvesting of shellfish in the Bay, clams are frequently collected, particularly adjacent to a small freshwater outflow, by members of the local population and consumed without reported ill effects.

The principal objective was to examine potential spatial heterogeneity in toxin levels in the soft-shelled clam *Mya arenaria*. Such differences could conceivably be used to explain variation between single "point-source" samples taken for the toxin monitoring program, and from nearby stations along a horizontal transect. To examine the effects of time-dependent exposure to the causative dinoflagellate *Protogonyaulax tamarensis* through submergence, toxin variations were also compared along a vertical transect extending from the high to low intertidal zone, during a period in late summer when toxin levels in shellfish and dinoflagellate concentrations in the water column are usually maximum.

As a secondary objective, seasonal differences in PSP toxins were determined on a weekly basis, over the normal ice-free season for the harvesting of wild clam stocks (May to November). The quantity and spectrum of toxins retained by the shellfish were determined by means of high-performance liquid chromatography and the results compared with the conventional bioassays.

ACCUMULATION OF SILVER FROM THE ALGA *ISOCHRYSIS* SP. BY THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*

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Studies conducted during 1984–85 showed that oysters accumulated silver (Ag) dissolved in water, but not absorbed to sediments; conflicting results were obtained to their ability to accumulate Ag from the alga *Isochrysis* sp. (Tahitian; TISO). Subsequently, six groups of 50- to 65-mm ($\bar{x}$ = 57 mm) hatchery-reared oysters (0.34 to 0.81 g initial dry meat weight) were exposed to Ag dissolved in water or Ag-laden TISO as food. Before and after a 4-hr feeding period each day, feces and pseudofeces were removed from the tanks. After 2 weeks, oysters, feces, and phytoplankton were analyzed for Ag content.

The Ag content of oysters exposed to dissolved Ag averaged 8.08 $\mu g\ g^{-1}$, but those fed contaminated algae contained only 2.01 $\mu g\ g^{-1}$, not significantly different from the Ag content of controls (1.50 $\mu g\ g^{-1}$). The total quantity of Ag provided each tank was nearly equal; 1120 μg for dissolved Ag and 1050 μg for TISO, but 90 μg was removed by oysters receiving dissolved Ag vs. 6.1 μg in algal tanks. Feces concentrations differed also; 32 $\mu g\ g^{-1}$ from controls, 50 $\mu g\ g^{-1}$ from oysters in dissolved Ag, but 201 $\mu g\ g^{-1}$ from oysters fed contaminated TISO. Ag eliminated in feces accounted for 95% of the total Ag offered in food.

The availability of metals to oysters may depend on the metal binding sites within phytoplankton cells. A phytoflagellate such as TISO may be able to bind metals more tightly than other types of phytoplankton. Further investigation is needed.

BIVALVE GROWTH AND FEEDING

FEEDING BEHAVIOR OF BLUE MUSSELS: EFFECTS OF MICROCROALGAL ECTOCRINES

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Evidence is presented which indicates that nontoxic microalgal ectocrines mediate the feeding behavior of the blue mussel *Mytilus edulis* (L.). Monoclonal cultures of six species of marine microalgae were grown in the laboratory on Guillard's f/2 media to the end of their exponential growth phase. Microalgal cells were removed from cultures by gentle filtration, leaving dissolved ectocrines in culture filtrates. Full strength filtrates and dilutions of filtrates (1/10 and 1/100) were then used to assay effects of dissolved ectocrines on filtration rate of mussels, using a non-static, flow-through apparatus.

Bioassay results show that dissolved ectocrines significantly affect filtration rates of mussels, depending upon microalgal species and concentration of filtrate used. Stimulatory and inhibitory effects of certain filtrates on filtration rates of mussels, however, were different than effects of the same filtrates on particle selection by mussels reported previously. Comparison of these effects will be discussed. Further experiments are being conducted to fractionate culture filtrates and determine the chemical nature of stimulatory and inhibitory substances.

DEVELOPMENT OF A MODEL TO SEED MUSSEL BOTTOM LEASES TO THEIR CARRYING CAPACITY—PHASE I RESULTS

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Model predictions and field data indicate that 25% of the available food can be removed from the benthic boundary layer above a mussel bed path length of over 1 meter at current speeds of 3–5 cm/sec. Growth in relation to patch position was significantly less in the middle of large (over 10 m) patches relative to the edge. Large-scale depletion effects were also noted: in a 500m transect across 3 seeded sections on the flood tide in a low current area, food availability was lower in the inner vs outer sections (44.2% less phytoplankton cells, 32.2% less carbon, 21.5% less nitrogen). Mussel feeding selectivity accounted for 40% greater filtration rates on chlorophyll vs non-chlorophyll cells, but there appeared to be a threshold of number or percent chlorophyll cells for selectivity to occur. Selectivity occurred in all particle size classes of 3–5, 5–8, 8–10 and 10–15 μm in equivalent spherical diameter. Highest mussel feeding rates occurred during the fall phytoplankton bloom (.17 μg chlorophyll a min^{-1} g dry $meat^{-1}$, and lowest rates (30-fold less) were correlated with periods of low food availability during the summer.

Flume experiments and direct measurements of mussel height off the bottom were used to determine bottom roughness in a mixing model. Development of a computer model with further refinements is proposed in Phase II of the research, along with detailed examination of mussel seeding technology and mussel feeding thresholds.

AN *IN SITU* ESTIMATION OF THE EFFECT OF WIND-DRIVEN RESUSPENSION ON GROWTH OF THE MUSSEL, *MYTILUS EDULIS*

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Particles resuspended from the bottom form complex mixtures of variable quality which have been shown to be both benefical and detrimental to suspension feeders. Laboratory feeding experiments generally involve selected experimental conditions (e.g. size sorting, lack of spatio-temporal variability) that produce poor simulations of natural suspensions. Ideally, experiments should involve *in situ* growth comparisons between adjacent areas with high and low resuspended loads (e.g. at different heights above the bottom). However, a complication of these field experiments is that phytoplankton depletion above dense suspension feeder beds causes additional variation in the particle field.

We attempted to circumvent this problem by measuring growth of *Mytilus edulis* (Pointe Mitis, St. Lawrence Estuary) using two independent methods, one including resuspended food supplies (growth experiment) and the other excluding this food source (energy budget scope for growth in calm weather only). In the growth experiment, triplicate groups of mussels were placed within a natural mussel bed (0 m) and at 1 m above bottom in a zone of greatly reduced resuspension. Observed growth was therefore attributable to both resuspension and phytoplankton. Scope for growth, based on particles pumped from 0 and 1 m, was attributable to utilization of phytoplankton. Ratios of growth at both levels were computed for each method. Compared to scope for growth in a calm water column, observed growth in the presence of resuspension was reduced by 24–40%.

GROWTH RATE OF HARD CLAMS, *MERCENARIA* SPP., FROM THE INDIAN RIVER LAGOON, FLORIDA, AS DETERMINED BY INTERNAL GROWTH LINE ANALYSIS

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The Indian River Lagoon on the east central coast of Florida is a significant source of hard clams, *Mercenaria* spp., for the commercial trade. The industry which has developed to support this trade is an important contributor to the local economy. There is considerable concern within the industry that natural sets of hard clams will not be sufficient to continue to support the fishery. Consequently, much effort is being expended to develop hard clam aquaculture on a scale sufficient to supplant natural populations as the primary source of stock.

More than 700 shells of hard clams from a variety of habitats throughout the lagoon were sectioned for analysis of internal lines to determine age and growth rates of the regional stock. Results of this study indicate that first year growth is extremely rapid. However, growth rate varied considerably from area to area within the lagoon. Variations in growth related to time, habitat, and genetics composition are considered.

SITE AND HYDROGRAPHIC FACTORS INFLUENCING THE GROWTH OF *MERCENARIA MERCENARIA* IN LONG ISLAND SOUND (LIS)

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We have characterized the environment at three sites in LIS, chosen to investigate factors affecting settlement and growth of the hard clam, *Mercenaria mercenaria*. The sites, near Greenwich, Milford, and Stonington, CT, were selected to represent diverse ecological conditions within LIS. Age analysis of shells of live clams from the sites indicates and even distribution of all year classes from 0+ to over 50. Sand substrates were similar at all sites, but gravel was heavily interspersed in Greenwich sediment, and shell debris at Milford. Seawater temperature averaged 3°C lower at the Stonington site. Sites at Greenwich and Milford are characterized by low average current flow (0.0–0.5 knots) and high primary productivity (0.5–2.0 fluorescence units). The Stonington site had high average current flow (0.3–1.0 knots), and low levels of productivity (0.1–0.9 fluorescense units). Oxygen levels were close to saturation throughout 1987 at Milford and Stonington. At Greenwich, oxygen levels fell to about 50% saturation (4.2 ppm) between July and August. Measurement of biological oxygen deman (BOD) averaged about 3.0 ppm higher at Greenwich and Milford than at Stonington. The importance of major site and hydrographic conditions are discussed in relation to the growth of caged clams and survival of unprotected clams.

CRUSTACEANS

DREDGING AND DUNGENESS CRABS: IMPACT ASSESSMENT AND MITIGATION

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Grays Harbor, Washington, is a major center for the Dungeness crab fishery in the state, and impacts to the crab resource, particularly from dredging, are a primary concern related to the proposed widening and deepening of the existing navigation channel. In a series of meetings with agency representatives, crab biologists, and crabbers, an approach to this problem was developed which included modification of a hopper dredge draghead to reduce impacts, collection of additional entrainment data, and evaluation of a mitigation technique.

The Seattle District, U.S. Army Corps of Engineers, conducted entrainment studies in Grays Harbor to assess the effectiveness of a modified draghead in reducing crab entrainment. In addition, trawl samples were taken simultaneously with entrainment samples for comparison of entrainment rates with crab densities in the navigation channel. These data were incorporated into a computer model for predicting crab losses due to dredging. The results have been used, in conjunction with previous studies on crab habitat preference, to formulate a suitable mitigation plan utilizing oyster shell. The role of these environmental studies in the planning process is also discussed within the context of applicable federal statutes and Corps of Enginners regulations.

ENTRAINMENT OF ESTUARY ORGANISMS BY HOPPER DREDGING

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A proposal to deepen the entrance channel at the mouth of the Columbia River (MCR) raised concern over the entrainment of Dungeness crab by hopper dredging. A study was begun in 1984 by Portland District Corps of Engineers to determine the number and age of Dungeness crab entrained and whether entrainment was correlated with any dredging or environmental parameters. Studies were done with a sampler developed for the Corps of Engineers hopper dredge *Essayons*. Samples have been collected throughout the April to October dredging season at the MCR. Results to data have shown the young of the years Dungeness crab (7-25mm) can be entrained in large numbers when they are abundant at the MCR. However, adult and subadult crabs have never been collected in large numbers. No relationship between entrainment and any other dredging or environmental parameter tested was apparent except direction of dredging and tidal stage. In 1985, the least number of young of the year crab were collected when dredging against the flood tide and the largest were collected while dredging against the ebb tide. This relationship was not apparent for the 1986 or 1987 data. Additional studies are planned in 1988 to clarify this relationship.

THE EFFECTS OF SALINITY ON NITRITE TOXICITY IN THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN

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Toxic effects of nitrite appear to be a major factor causing decreased molting success in closed, recirculating systems used to produce softshelled blue crabs. The relationship between salinity and nitrite toxicity was investigated. Static acute toxicity tests with toxicant renewal were conducted on intermolt crabs and crabs undergoing ecdysis at different salinities. A nitrite concentration of 81 mg NO_2-N/L was used for shedding crabs and 105 mg NO_2-N/L was used for intermolt crabs. The percent mortalities of intermolt and shedding crabs exposed to these nitrite concentrations at different salinities was determined. Results indicate that high salinity decreases nitrite toxicity. Mortalities in commercial, closed shedding systems could be reduced by operating them at high rather than low salinity.

EFFECTS OF SUBSTRATE AND HARD CLAM DENSITY ON PREDATION BY PORTUNID CRABS

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Brachyuran crab predation on juvenile hard clams, *Mercenaria mercenaria*, constrains mariculture development on Long Island, New York. As part of a larger program on potential biological control of this predation, the feeding ecology of a locally abundant portunid crab *Ovalipes ocellatus* was examined and compared with that of the blue crab, *Callinectes sapidus*. Crab foraging behavior was observed in the laboratory on three substrates: sand (>800 μm); sand and gravel aggregate (<17 mm); and sand with natural shell debris. At a low density of juvenile (15–20 mm) clams, both species of crabs foraged most successfully in sand. *O. ocellatus* had the least success in sand with shell debris while *C. sapidus* was least successful in the sand with gravel substrate. Density experiments were conducted for *O. ocellatus* feeding on clams at five densities between 24/m^2 and 120/m^2 in sand with and without shell debris. The mean number of prey consumed over 48 hours was 10 to 64% greater in sand for all prey densities. Examination of clam mortality on a proportional basis indicated a low density prey refuge existed only in the sand with shell debris. A strategy of planting 15 to 20 mm hard clams at a low density (<24/m^2) on substrates with natural shell debris may therefore increase clam survival in the field grow-out stage where portunid crabs are significant predators.

SPATIAL ASPECTS OF FORAGING IN *CALLINECTES SAPIDUS*—IMPLICATIONS FOR SOFT-SEDIMENT MARINE BENTHIC PREDATOR-PREY DYNAMICS

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Two key components of predation, the functional response—where predators increase prey consumption as prey abundance increases—and the aggregative response—where predators congregate in areas of high prey density—may be density-dependent and vary as a function of environmental features. However, few

studies have addressed the interactive effects of these components upon predator-prey dynamics.

This study investigated (1) patch use and the functional and aggregative responses of the blue crab, *Callinectes sapidus* Rathbun, to soft-shell clams, *Mya arenaria* Linne, in the laboratory, and (2) the main and interactive effects of prey density, prey species, and sediment type on mortality of *Mya arenaria* and *Macoma balthica* with field experiments in Chesapeake Bay.

Interference, the functional response type, and the aggregative response were inferred from the laboratory results. Both patch scale and predator density affected the shape of functional response curves. The results of a three-way ANOVA on field data indicated that proportional mortality differed among species type, sediment type, and clam density, with significant interaction effects between species and sediment type, and between species type and density. The results suggest the importance of complex biotic and environmental interactions for soft-sediment marine benthic predator-prey dynamics.

TEMPERATURE-PROTOPERIOD CONTROL OF SPAWNING BY AMERICAN LOBSTERS: A FACULTATIVE REGULATORY SYSTEM

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There is conflicting information on the role of temperature and photoperiod in the regulation of spawning by American lobsters. Some studies have shown a requirement for short days followed by long days, while in others there was no photoperiod requirement. To determine how environmental factors regulate spawning, we exposed mature lobsters to various combinations of temperature and photoperiod. Under winter seawater temperatures typical of nearshore lobster habitat (0–5°C), there was no requirement for specific photoperiods. Spawning occurs in July irrespective of photoperiod regime (very short days, long days, decreasing spring daylengths or a delay in increasing daylengths). However, when winter temperature was elevated (13–14°C), spawning came under the influence of spring photoperiod. Lobsters required a change from short to long days in order to spawn and the long photophase had to be 12 hr or longer. No spawning occurs under constant short days (8 hr), or when long days are 10 hr. At long daylengths of 12 hr, 25% spawn and at 14 or 16 hr, 60% spawn. It therefore seems that vitellogenesis and spawning of near-shore lobster populations is normally regulated by seasonal seawater temperature, but that photoperiod can assume a regulatory role if the winter seawater temperature remains abnormally high. However, the high incidence of reproductive failure (40%) under elevated temperature and photoperiod indicates a less favorable environment for ovary maturation than is provided by low winter temperature.

FUNCTIONAL ANATOMY OF SNOW CRAB *(CHIONOECETES OPILIO)* REPRODUCTIVE SYSTEMS, AND A HYPOTHESIS FOR FERTILIZATION

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To help elucidate the reproductive characteristics of Atlantic snow crab, the functional anatomy of the male reproductive system and the female spermatheca was investigated using histological, transmission and scanning electron microscopic techniques, and microscopic observation of fresh material.

In addition to correcting earlier presentations of spermatozoan structure in this species, several new observations were made. The spermatozoa and the matrix of the anterior vas deferens are packed into spermatophores and surrounded by a pellicle which appears to be secreted by the cells lining the anterior vas deferens proximal to the testis. The highly-folded configuration of this pellicle may act as a safeguard against dehiscence induced by contact with seawater during copulation. The posterior vas deferens contains two distinct secretions which are probably ejaculated along with the spermatophores and the anterior vas deferens matrix.

Anatomical and *in vitro* observations suggest that fertilization is initiated by exposure of the spermatophores to a hypotonic medium. Such a medium may be generated within the spermathecae by dilution of the seminal fluids/spermatophore storage matrix with seawater prior to egg mass extrusion. Devagination of the liberated spermatozoa may be facilitated by the same mechanism.

APPLICATIONS OF MOLECULAR GENETICS TECHNIQUES FOR UNDERSTANDING BLUE CRAB LIFE HISTORY DYNAMICS

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Recent advancements in the field of molecular genetics have led to applications of mitochondrial DNA (mtDNA) restriction morph analysis for population genetics studies. mtDNA generally evolves much more rapidly than nuclear DNA and changes in the mtDNA molecule are incorporated through populations relatively rapidly. These properties make mtDNA a sensitive indicator of geographic structuring of populations.

Blue crabs (*Callinectes sapidus*) have a complex life history that involves both planktonic larval stages and motile adult stages that results in sojourns in oceanic and estaurine waters. There seems to be a concerted effort between this complex life history and physical processes (prevailing winds and movement of water masses) to maintain the integrity of blue crab populations of major estuarine systems. If this is the case, populations of blue crabs from major estuarine systems may be distinguishable by mtDNA restriction morph analysis. We are conducting a preliminary analysis of mtDNA restriction morphs of blue crabs within the lower Chesapeake Bay. We will report on these preliminary studies and discuss the potentials of using this technique for understanding life history dynamics of this important species.

QUALITY OF SHELLFISH GROWING WATERS

THE QUALITY OF SHELLFISH GROWING WATERS IN THE GULF OF MEXICO

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Classified shellfish growing waters in the Gulf of Mexico were examined as an indicator of water quality. Information was compiled on the administration of state programs, status of classified waters, sources of pollution affecting harvest-limited waters, and trends in classification between 1971 and 1985. Data were collected by site visits to the five Gulf states, through interviews with state personnel, and by reference to written materials. These results may provide guidance to national and regional decisionmakers in the development of policies and implementation strategies to maintain and, in some cases, improve estuarine water quality.

The majority of shellfish growing waters in the Gulf of Mexico do not meet the fecal coliform standards for approved harvest. Twenty-nine percent of waters are classified as prohibited. Twenty-seven percent of waters are managed as conditionally approved and are affected by freshwater inflows from heavy rainfall or high river stages. The most productive oyster reefs are found in these conditionally approved waters.

Across the Gulf of Mexico, the predominant sources of fecal coliform are sewage treatment and collection systems (a contributing factor in the closure of 34 percent of harvest-limited waters from primary sources and 22 percent from upstream sources), septic systems that do not function properly in coastal areas because of poor soils and high groundwater tables (39 percent and 10 percent upstream), and stormwater runoff from urban areas (33 percent and 32 percent upstream). Overall, upstream sources affect 57 percent of harvest-limited areas. Contributions from wildlife are significant in rural estuaries (21 percent and 3 percent upstream). Runoff from pasturelands affects estuaries in Louisiana and Texas (8 percent and 27 percent upstream). Straight pipes are a problem in coastal Louisiana (13 percent). Actual effects from industry (10 percent) and boating and shipping activities (7 percent) are minimal compared to other sources.

The major trend to occur in the Gulf region is an increase in waters managed as conditionally approved. This change is a result of increased monitoring efforts, stricter compliance with the NSSP manual, and heightened awareness of nonpoint sources.

SHELLFISH GROWING AREAS IN NEW YORK STATE: CURRENT STATUS AND TRENDS

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New York State's Marine District encompasses about 1.2 million acres of marine and estuarine shellfish growing areas. Approximately 17% of the shellfish lands are closed (uncertified) to harvesting due to coliform contamination in excess of New York and National Shellfish Sanitation Program (NSSP) criteria. Pollution sources are major sewage treatment plant discharges and stormwater runoff in western sections and runoff and other nonpoint sources in central and eastern Long Island.

Thirty-eight percent (38%) of the 380,000 acres of productive inshore waters are uncertified. The closures generally follow the pattern of increasing population, from 100% closed in the New York metropolitan area to 71% in Nassau County and 10% in Suffolk County.

The short-term trend in New York's shellfish growing areas will likely be towards small closures in understudied areas or in areas of intense development pressure. Some embayments have not been sufficiently evaluated under "worst case" hydrographic

and meteorological conditions as required by the 1986 revision of the National Shellfish Sanitation Program (NSSP), and may fail reevaluation under wet weather conditions.

Long-term trends are more difficult to predict. While there is an increasing awareness of how land and water use policies affect water quality, the future of New York's growing areas will depend on the ability of state and local governments to implement mitigation practices such as upgradings of sewage treatment plants, installation and use of marine pumpout facilities and control of stormwater runoff.

SHELLFISH RESOURCE DEGRADATION AS A FUNCTION OF LAND USE PRACTICES

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Environmental degradation with respect to shellfish resources is becoming a serious problem on Cape Cod as a direct result of rapid coastal development. Over 5,000 acres were closed to shellfishing in 1987 compared to 712 acres in 1980. Closures were due to bacterial contamination from such sources as stormwater runoff, inadequate on-site septic systems and warm blooded animals. In addition, shellfish habitat is being lost due to eutrophication from nutrient enrichment caused by the cumulative effects of current land use practices. Individual communities and the entire county are beginning massive educational and action-oriented programs to ameliorate the situation. But research is needed in a wide range of disciplines to maintain high water quality standards and a viable shellfish industry.

CONTAMINANT DISTRIBUTION IN OYSTERS AND SEDIMENTS FROM THE GULF OF MEXICO

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Polynuclear aromatic hydrocarbons (PAH), chlorinated pesticides and PCBs were determined in oysters (*Crassostrea virginica*) and sediments as part of NOAA's Status and Trends mussel watch program to provide information on the current status of the concentration of these contaminants in Gulf of Mexico coastal areas removed from point sources of input. Coprostanol analyses of sediments shows that anthropogenic materials are associated with the sediments from most the stations sampled. It was concluded from the first year data from this program that the levels of contaminants encountered are low compared with areas near point sources. Average PAH concentrations are nearly the same in oysters and sediments, although the molecular weight distribution is different. Average pesticide and PCB concentrations are higher by a factor of 10 to 130 in oysters as compared to sediments. Continued sampling and analyses for Year II (and possibly Year III) for long-term trends in the concentrations of these contaminants in oysters will also be described.

PATTERNS AND RELATIONSHIPS OF TRACE ORGANIC AND METAL DISTRIBUTIONS IN BIVALVES AND SEDIMENTS FROM THE PACIFIC AND ATLANTIC COASTS

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The NOAA Mussel Watch Program, one component of the National Status and Trends (NS&T) Program, is a marine monitoring program that relies on repeated, precision sampling and chemical analyses of sentinel organisms. The goal of Mussel Watch is to quantify the current status of environmental quality of the nation's coastal and estuarine regions and measure long-term spatial and temporal changes in concentrations of environmental contaminants. Data generated through the NS&T Program will be used to establish a high-quality, fully interpreted national database, thus providing a foundation for environmental management decisions and for testing scientific hypotheses on future marine pollution impacts.

Mussels or oysters and depositional sediments have been collected at more than 100 Atlantic and Pacific coastal sites during the first three years of the program. Organic chemical measurements of PAH, PCB, and 16 pesticides and 17 trace and major metals have been completed on samples collected during year one and two. Highest levels of organic contaminants on the East Coast (New York Harbor, Boston Harbor, and Buzzards Bay) and on the West Coast (San Diego Bay, San Francisco Bay, and Elliot Bay) are not coincident with the locations of the highest trace metal concentrations. In general, Pb and Hg concentrations were found

together with high organics, but levels of Ag, Zn, Cu, Cd, and other metals were decoupled with respect to organic contaminants. Patterns and relationships among chemical parameters (e.g., lipids, TOC, etc.) will be discussed.

TRIBUTYLTIN CONTAMINATION IN BIVALVES FROM U.S. COASTAL ESTUARIES

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Organotin compounds have a range of toxicity and as such have found a broad spectrum of applications including use as fungicides, bactericides, pesticides, anticancer agents, and biochemicals. Tributyltins (TBT) have in recent years become a major component of many antifouling paints because they are 10 to 100 times more effective than copper-containing paints. The fact that TBT impact non target organisms has led to environmental concern about these compounds.

Oysters (*Crassostrea virginica* or *Ostrea sandwichensis*) and mussels (*Mytilus edulis*) from U.S. coastal waters were found to be contaminated with TBT and its less toxic breakdown products (dibutyltin and monobutyltin). The concentration of TBT range from <5 to 1560 (366 avg.) ng $\cdot$ g^{-1} dry weight as tin and accounts on average for 74% of the tin present as butyltins. Replicate oyster samples from a specific site concentrate TBT to the same level. Concentrations of TBT found in oysters varied both spacially and temporally. No apparent differences were seen in oyster and mussel ability to concentrate TBT from their environment. Oysters and mussels are therefore excellent sentinel organisms to monitor the environmental levels of TBT available to marine organisms.

HARD CLAM TRANSPLANTS IN NEW YORK STATE

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The State of New York has had an active shellfish transplant program since 1964. During this time the program has been successful in moving over one-half million bushels of hard clams from closed (uncertified) shellfish lands in both public and private transplant activities. Transplants have typically been from uncertified waters in the western Long Island-New York metropolitan area that have little potential for reclamation for direct market harvesting.

The purpose of New York's program is twofold: first, public health is protected by reducing the resource available for poaching in polluted areas; and second, after a twenty-one day cleansing period in certified waters, the shellfish may be harvested for market purposes. Additionally, large sized hard clams have been transplanted to increase the spawning stock in receiving waters.

Transplants have accounted for greater than 10% of New York's annual hard clam harvest in both 1986 and 1987. Each of these years has seen over 30,000 bushels of clams relayed from closed areas for cleansing, mostly to privately held lots in Great South Bay or the Peconic-Gardiners Bay system. Prior to this, transplants resulted in large quantities being relayed to "public" underwater lands in government funded projects.

Transplants require constant supervision to ensure that shellfish do not bypass the cleansing process. The state monitors all aspects of the program, from harvesting to replanting on the relay site. Participating private interests or local government authorities are responsible for ensuring that shellfish remain in certified waters for the duration of the cleansing period.

USING BIOENERGETICS OF INTERTIDAL OYSTER POPULATIONS AS A MEASUREMENT OF ANTHROPOGENIC PERTURBATIONS TO SHELLFISH GROWING WATERS

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Shellfish growing waters, such as salt marshes and estuaries, adjacent to urban sprawl receive a myriad of wastes and other inputs previously foreign to these sensitive coastal ecosystems. The stress created by this heterogeneous group of anthropogenic substances, and the continual fluctuation of inputs, may prove much more difficult for an ecosystem to acclimatize to than it would for a single pollutant. Because oysters are sessile, benthic, and feed by filtering large volumes of water, they serve as "sentinels" of, and are directly affected by, the quality of water passing over them. For this reason, sub-lethal changes in oyster

scope for growth can infer that alterations in their surrounding environment have occurred. This presentation will describe methods of a study, recently initiated, to examine sub-lethal effects of coastal development on the ecophysiology of intertidal oyster populations in the North Inlet Estuary, SC. Methods discussed will include *in situ* measurements of oyster scope for growth, O:N ratios, biochemical composition, seston food quantity and quality, recruitment, juvenile survival, and susceptibility to parasitic diseases such as "Dermo" and "MSX". Anticipated accomplishments and benefits of studies of this design are to elucidate the effects of coastal development on shellfish growing waters in terms of 1) nutrient storage, 2) fecundity, recruitment, and juvenile survival, 3) susceptibility to disease, 4) scope for growth, and 5) overall energetics of oysters.

A REVIEW OF THE OCCURRENCE AND PERSISTANCE OF ENTEROVIRUSES IN THE MARINE ENVIRONMENT

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There are greater than 114 different viruses known to be excreted in human feces at concentrations approximately 1 million per gram feces. It is necessary to assess levels of enteroviruses, and to develop management strategies for the maintenance of environment quality. Research has demonstrated that enteric viruses occur and can be transported to shellfish and their natural growing waters. Many environmental factors may enhance or detract from the persistance of these viruses in the marine environment.

Viruses may be transported to shellfish and their natural growing waters by numerous routes. Domestic sewage is the main route into the marine environment. Many viruses survive secondary sewage treatment and chlorination leaving significant numbers of infectious viruses that may reach the marine environment by either direct discharge of treated or untreated sewage effluents. Additional routes of transportation include ocean dumping, aerosols, runoff, septic tanks and pipe leakage, groundwater and others.

After viruses are released into the coastal waters, they may remain suspended in seawater and be transported to recreational areas or accumulate in bottom sediments or bioconcentrate in filter-feeding shellfish. Certain viruses can persist for long periods of time in the environment. Many environmental factors may affect virus survival: physical—temperature, light, aggregation and adsorption; chemical—pH, chemicals; biological—virus type, bacterial activity.

RELATIONSHIPS BETWEEN BACTERIAL INDICATORS, BACTERIAL PATHOGENS, AND ENVIRONMENTAL PARAMETERS IN SHELLFISH HARVESTING WATER

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Standards for shellfish harvesting waters are established according to fecal coliform levels in the seawater. Despite this precaution, the incidence of oyster-borne gastroenteritis is increasing. Information demonstrating statistical relationships between fecal coliform levels, other bacterial indicators, and pathogenic bacteria is lacking. Therefore, oysters (*Crassostrea virginica*), seawater, and sediments were quantified for total and fecal coliform, fecal streptococci, *Clostridium perfringens* spores and vegetative cells, and pathogenic *Vibrio* species. In addition, various environmental parameters (salinity, temperature, dissolved oxygen, etc.) were measured. It was determined that more representative counts for all bacteria were obtained from the sediments than from the overlying waters. It was also concluded that there is no correlation of *Vibrio* species with indicator bacteria in seawater, oyster meats, or sediments.

BENEFICIAL APPLICATION OF THE CONDITIONALLY APPROVED CLASSIFICATION FOR SHELLFISH GROWING WATERS

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Many productive shellfish areas have been closed prohibiting the taking of shellfish for direct consumption in order to protect public health. Such closures have frequently resulted in economic hardship to the shellfish industry, loss of recreational opportunities and neglect of a valuable, renewable, natural food resource.

In the early 1970's, Connecticut's shellfish industry was beginning to rebound after decades of decline when they were faced with a potential closure of their prime marketing beds. Water samples from this growing area showed episodic elevated levels of coliform indicators exceeding the NSSP standard for approved classification. Implementation of a permanent closure for this area would have severely curtailed the resurgence of Connecticut's shellfish industry and eliminated the State's major recreational shellfishing grounds.

A potential alternative to permanent closure of these shellfish beds existed. *The NSSP Manual of Operations, Part I* provides for a "conditionally approved classification" of a shellfish growing

area if the pollution causing event can be predicted. In 1978, an extensive sanitary survey was executed cooperatively by State, local and industry officials, demonstrating that this valuable resource area met the criteria for conditionally approved status. Initial data collection required considerable investment of time and money. A decade later, Connecticut has developed a significant shellfish industry and recreational shellfishery as a direct result of that investment.

THE CLASSIFICATION OF SHELLFISH GROWING WATERS FROM THE BAYMEN'S PERSPECTIVE: ARE THEIR COMPLAINTS LEGITIMATE?

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Over the past 50 years, failure of shellfish growing areas to meet National Shellfish Sanitation Program water quality harvesting standards has resulted in the closing of approximately 19% of New York's 1 million acres of marine waters to shellfish harvesting. Closures have had negative economic and social impacts and now threaten the continued viability of the State's shellfish industry. Independent baymen, who account for nearly all of the State's shellfish production, are antagonistic toward the shellfish growing area classification program; this manifests itself in a variety of ways, including poaching and legal action to overturn closure decisions. Classification is, thus, a major source of conflict between baymen and classification program officials.

The objections by the baymen to the classification program fall into two broad categories: (1) the coliform bacteria standard, which is the basis for closure of shellfish areas, is invalid on several counts causing areas to be closed when they should be open and (2) all the emphasis of the classification program is placed on prohibiting shellfishing rather than correcting the causes of the closure. Program managers tend to dismiss baymen's objections as self-serving and ignore their possible legitimacy, while baymen complain that program managers are unresponsive and unsympathetic. Because the classification is so controversial, and to provide insights into baymen-program management dynamics, a critical assessment of the classification program was made from the baymen's perspective.

Review of published data and an analysis of the classification program itself provides support for the objections raised by the baymen. Thus, while the baymen may appear to be solely motivated by economic self-interest, there is a rational basis for the baymen's position—many baymen, in fact, are at least superficially aware of inconsistencies in the program. This legitimizes, in part, the baymen's view that regulatory officials are anti-baymen, and why they show little support for the classification program, and tacitly approve poaching. It means that regulatory officials must begin to address the baymen's complaints. More importantly, it may mean the classification program is flawed and not adequately protecting public health.

NATIONAL COLLABORATIVE STUDY OF THE RELATIONSHIPS OF INDICATORS, HUMAN ENTERIC PATHOGENS AND POTENTIAL HEALTH RISKS IN SHELLFISH AND GROWING WATERS

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Classification of shellfish growing waters is meant to insure the sanitary quality of shellfish by monitoring raw sewage contamination of these waters. It is based on an allowable limit of fecal coliform bacteria in the growing waters because shellfish are "filter-feeding" organisms. Problems with the current method of classification of shellfish growing waters have caused significant lack of confidence in the system by industry, regulatory officials, university researchers and the consumer public. The need for a national collaborative study to re-evaluate the methods used for growing water classification has been advised for many years in meetings and workshops by all groups concerned.

This project will be a four year collaborative study to evaluate the current relationships between indicators of sewage contamination, and human enteric pathogens within a total environmental assessment of commercial shellfish growing areas. The relationships of these parameters of potential public health risk will also be evaluated. It will be determined if the current shellfish fecal coliform standards and guidelines are still the most valid and reliable indicators of potential health risk from sewage-related enteric pathogens in the sanitary and epidemiological conditions existing throughout important shellfish growing waters in this country today.

The study will involve university, federal, state, local and industry personnel from four main shellfish growing areas in the country—North Atlantic, South Atlantic, Gulf coast and Pacific coast.

GENETICS

ABNORMAL GAMETOGENESIS IN TRIPLOID AMERICAN OYSTERS CRASSOSTREA VIRGINICA

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Diploid and triploid sibling oysters were examined histologically at intervals during the reproductive season of their third year. By mid-July, gametogenesis had progressed in diploids and triploids so that the sex of all individuals was distinguishable. At this stage, diploids of both sexes displayed a full range of normal development. Diploid males produced spermatids and spermatozoa while diploid females had development ranging from young ovocytes to mature primary ovocytes.

In July, triploid males had macroscopically visible gonadal development. Follicular development was not inhibited by triploidy. There was a proliferation of primary spermatocytes but an absence of spermatids and spermatozoa. Males were less inhibited by triploidy than females. Triploid females displayed some ovogonial proliferation but very few primary ovocytes developed.

By mid-September, triploid females were characterized by underdeveloped follicles with some containing one to a few mature primary ovocytes. Conversely, late season triploid males had well developed follicles filled with primary spermatocytes. Diploids, at this time, were fully ripe and some individuals had spawned.

GROWTH RATE OF SIBLING DIPLOID AND TRIPLOID OYSTERS, *CRASSOSTREA GIGAS*

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The rate of growth over two years has been compared between diploid and triploid Pacific oysters. Diploid and triploid siblings originated from a single mass spawn and were maintained in vexar bags for grow-out at six intertidal sites in California and Washington by Coast Oyster Company. Preliminary analysis suggests that the rate of growth of triploid oysters exceeds that of diploids in environments characterized by reduced levels of suspended particulate matter. In more productive environments, no growth rate differences have been observed.

Energetic analyses conducted in the laboratory on starved and fed members of this cohort suggest that differential utilization of glycogen may lead to observed differences in growth rate. These results are discussed with respect to the physiological energetics of diploid and triploid oysters.

INDUCED TRIPLOIDY IN *MERCENARIA MERCENARIA* L.: EFFECTS ON PERFORMANCE IN THE JUVENILES

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Triploid hard-shelled clams were produced in the spring of 1984 by treating fertilized eggs with 0.5 mg/liter of cytochalsin B. After three growth seasons, triploid clams were significantly smaller than diploid controls with respect to dry tissue weight and all shell parameters. However, significant differences in shell allometry, ratios of shell length and height to shell inflation, were evident. Comparative performance is now being traced through the 5th growth season. These findings are discussed relative to those for other bivalve species produced as triploids.

SELECTIVE BREEDING FOR RAPID GROWTH IN *MERCENARIA MERCENARIA:* EARLY GROWTH AND SURVIVAL OF HIGH AND MEAN-SELECTED LINES

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Hard clams *(Mercenaria mercenaria)* from Folly River, SC, were spawned in 1983 to produce an F_1 generation. At 2 years, the size distribution of the population was determined. The largest 10% ($x = 47.5$ mm) and an equal number of mean size (36.9 mm) were chosen as broodstock for high and mean selected lines. In Spring 1986, 3 breeding trials were conducted, each producing a high and mean F_2 line. In each trial, early growth of high and mean lines was similar, but high lines grew slightly faster in the nursery stage. At 18 months of age, high lines were 1–15% larger than mean lines. Larval survival was similar in high and mean lines, but high lines suffered higher mortalities at metamorphosis and during the early post-set period. Lines were sampled at 3, 9 and 15 months for electrophoresis. Although 150 brookstock were used for each breeding trial, actual numbers of spawners varied from 12 to 90. These parents are being sampled non-destructively for determination of allozyme frequencies. At 2 years of age offspring will be sampled for electrophoresis and genotypes compared to those of the parents to identify parents of fastest-growing or best-surviving offspring. These parents will be respawned to produce a different F_2 generation. The largest of the original F_2 high lines will be spawned in Fall 1988 to produce F_3 generations.

VARIATIONS IN ALLELIC FREQUENCIES IN JUVENILES OF THE HARD CLAM, *MERCENARIA MERCENARIA*

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Mercenaria mercenaria, the northern hard clam or quahog clam, has long been an important species for commercial and recreational shellfishing and may now be commercially cultured. Genetic improvement of the mariculture breeding stock of clams could greatly enhance economic return. The leucine aminopeptidase *(Lap)* locus has been extensively studied in marine bivalves, especially *Mytilus edulis* where one allozyme contributes to differential mortality of recent set through its higher catalytic efficiency and greater nitrogen loss under low salinity stress. This study was initiated to examine potential differential survival in *M. mercenaria* juveniles from a Mendelian across at the *Lap* locus under laboratory conditions. Individuals heterozygous for the Lap^{100} and Lap^{96} alleles were crossed and the offspring split into ambient salinity (≥30‰) and reduced salinity (22‰) seawater and then reared under standard hatchery and nursery conditions. Survival of the crosses in ambient salinity seawater leveled off at approximately 1% after 70 days, while all clams in reduced salinity died. Juvenile clams originally reared in ambient salinity and subsequently transferred to reduced salinity also showed high mortality, although some allozyme data were collected from these clams. Horizontal starch gel electrophoresis with an aminopeptidase stain revealed allozyme phenotypes on individual clams. Although natural populations appear to be in Hardy-Weinberg equilibrium, resulting phenotypic ratios were significantly different from Mendelian expectation. These deviations were consistent from day 74 through day 206. The largest deviations observed were deficiencies of Lap^{100}/Lap^{100} homozygotes. There were no statistically significant differences observed between ambient and reduced salinity treatments. The Lap^{100} allele or a closely linked locus appears to act as a homozygous recessive with approximately a 50% mortality rate in the nursery.

DETERMINATION OF NULL ALLELE FREQUENCY AT AN ALLOZYME LOCUS IN A NATURAL OYSTER POPULATION

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To estimate the frequency of null alleles at the leucine aminopeptidase-2 *(Lap-2)* locus in a natural oyster *(Crassostrea virginica)* population, *Lap-2* phenotype, leucine aminopeptidase (LAP) activity, and total protein were measured in 312 oysters. Laboratory breeding experiments with oysters had previously suggested the existence of null (electrophoretically nonreactive) alleles at several allozyme loci, including *Lap-2*. Moreover, among the offspring of active/null heterozygous parents, active/null heterozygotes had about half of the LAP specific activity of active/active heterozygotes. Measurement of LAP specific activity was used for discrimination between active/null heterozygotes and active/active homozygotes with the same mobility phenotype on starch gels.

Of the 312 oysters, 106 were single-banded or "apparently homozygous" and 13 alleles were recognized. LAP specific activity was subsequently measured in the 106 single-banded oysters, and 29 of the 106 were re-classified as active/null heterozygotes based on low LAP specific activity values. In all instances, the activity data showed a bimodal distribution, with no overlap between the low activity class and the high activity class. Many (about 27%) of the single-banded oysters are actually active/null heterozygotes, so the electrophoretic screening by itself results in many misclassifications and an inflated estimate of the proportion of homozygous individuals. Before reclassification of the active/null heterozygotes there is a 4.8% deficiency of heterozygotes; after reclassification there is a slight (4.6%) excess of heterozygotes.

This result suggests that the presence of null alleles at high frequency may account for commonly observed heterozygote deficiencies in Molluscan populations.

GENETIC VARIABILITY IN POPULATIONS OF *CRASSOSTREA VIRGINICA* FROM THE NORTHERN GULF OF MEXICO

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Allelic variation at 23 presumptive gene loci was assessed among ten populations of *Crassostrea virginica* from the northern Gulf of Mexico, extending from Biloxi Bay, Mississippi, westward to Galveston Bay, Texas, using standard procedures of starch gel electrophoresis. Eleven of the 23 loci surveyed proved to be monomorphic across all population samples. The percentage of polymorphic loci among populations ranged from 0.238 in the Lake Calcalsieu, Louisiana, population to 0.428 in a Terrebonne Bay, Louisiana, sample with a mean of 0.321. Allelic variation at six gene loci, Aat-1, Icdh-1, Icdh-2, Mdh-1, Mdh-2, and Sordh, was limited to the occurrence of one or a few rare alleles usually in the heterozyous condition. Allelic diversity was consistently highest among all populations at six loci, Gpi, Lap-1, Lap-2, Mpi, Pgdh, and Pgm-1. Allelic distributions at the twelve variable loci were examined for evidence of population subdivision and the presence of potential genetic markers. Estimates of average heterozygosity among populations appeared to be slightly lower than reported for eastern Gulf coastal and Atlantic populations of this species.

OYSTER PARASITES

TECHNIQUE FOR PURIFYING *PERKINSUS MARINUS* HYPNOSPORES

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Perkinsus marinus, the etiologic agent of "dermo", is responsible for up to 50% mortality of market-sized oysters in Texas in most years. Detection of the agent and diagnosis is currently based upon a subjective examination of thioglycollate-cultured and stained suspect tissues. Quantitative techniques such as those which would quantify the amount of parasite material in oyster tissues or assess the number of hypnospores present in cultured tissue have suffered from a lack of an adequate procedure for purifying the agent. A technique was developed for extracting *P. marinus* hypnospores from infected oyster tissues based upon treating those tissues with 0.5% trypsin followed by 2 M sodium hydroxide. This technique provided a preparation of hypnospores free of oyster tissue and other parasitic organisms such as *Nematopsis*. The number of spores was further quantified using a coulter counter and the number of hypnospores per gram tissue related to the semiquantitative assessment of infection intensity obtained from the thioglycollate-culture method.

THE SPATIAL DISTRIBUTION OF *PERKINSUS MARINUS* IN RELATION TO ITS OYSTER HOST AND AN ECTOPARASITIC SNAIL *BOONEA IMPRESSA*

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The endoparasitic protozoan *Perkinsus marinus* is a major cause of oyster mortality in the Gulf of Mexico. The small-scale spatial distribution of *Perkinsus*, its oyster host, and a second oyster parasite, the snail *Boonea impressa*, was examined on two oyster reefs in Aransas Bay. Large oysters (>5 cm long) were infected 3 to 4 times as frequently by *Perkinsus* as smaller oysters. Infected oysters were less contagiously distributed (lower $s^2/\bar{x}$) than the entire oyster population although similar to the large component of the population in which most infections were found. The spatial distribution (Moran's I) of infected oysters, when different, was more nearly random than the distributions of the oysters or snails. The distribution of large *Boonea* explained the distribution of infected oysters better than any other parameter measured. Hence the influence of snail parasitism on *Perkinsus* prevalence and infection intensity, in large measure, determined the distribution of *Perkinsus* on these reefs. Feeding by *Boonea* transmits *Perkinsus* and increases infection intensity in infected oysters. Because *Perkinsus* may be responsible for half of all mortality in market-sized oysters, the distribution of snail patches may play an important role in the distribution of mortality in oyster populations.

A PARASITOLOGICAL SURVEY OF OYSTERS *(CRASSOSTREA VIRGINICA)* ALONG THE LOUISIANA COAST

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Oysters were collected from upper, mid and lower estuarine sites of four major oyster producing watersheds in Louisiana (Lake Borgne, Barataria Bay, Terrebonne Bay, and Lake Calcasieu) and examined for *Perkinsus marinus*, *Nematopsis prytherchi*, *N. ostrearum*, and *Bucephalus cuculus*. Histological sections were used to determine incidence of ciliates and nematodes at each site. Relative numbers of "pigment cells", gonad/body ratios and percent atrophic digestive diverticula were also determined using histological sections.

Comparisons were made between parasitism and condition of oysters in relation to salinity within and between watersheds. Higher percentages of oysters with atrophic digestive diverticular were found at the higher salinity sites. Increased levels of parasitism, rather than environmental pollutants, appear to be the cause of atrophy of the digestive diverticula.

DISTRIBUTION OF *PERKINSUS MARINUS* AND ITS EFFECT ON REPRODUCTIVE DEVELOPMENT IN OYSTER POPULATIONS IN THE GULF OF MEXICO

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The protozoan parasite, *Perkinsus (=Dermocystidium) marinus*, is responsible for high mortality in oyster *(Crassostrea virginica)* populations in the Gulf of Mexico each year. As part of NOAA's "Status and Trends" program, 60 oysters were sampled from each of 49 sites in the Gulf of Mexico from December to March over two years to determine the prevalence and the intensity of infection of *P. marinus*. Prevalence (% of sample infected) was higher in 1986 when only 1 site was <50% infected and 20 were 100% infected, compared to 1987 when 14 sites were <50% infected. Median intensity of infection ranged from 0 to 2.67 (1986), and from 0 to 1.67 (1987) on a 0 (uninfected) to 5 (highly infected) scale. Three regional foci of high *P. marinus* infection exist: the northeast and central coasts of Texas, central Louisiana, and southwest Florida. Factors significantly ($P < 0.05$) affecting the intensity of *P. marinus* infection include salinity, local agricultural land use, and local industrial land use. Oyster gonadal state was qualitatively rated on a scale from 1 (sexually undifferentiated) to 8 (spawned out). No relationship between intensity of *P. marinus* infection and sex or stage of reproductive development was found, probably because samples were taken during the winter months when the intensity of *P. marinus* infection is at a seasonal low.

AQUACULTURE

AN EXAMINATION OF STATE AQUACULTURE LEASING SYSTEMS IN THE UNITED STATES: ISSUES AND STRATEGIES

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The State of South Carolina has made a firm commitment to the development of the aquaculture industry. This is evident by the preparation of a "Strategic Plan" for aquaculture development. For culture operations that require the use of the state's public resources the Plan acknowledges that South Carolina does not have a leasing program in place to balance the needs of aquaculture with the public's rights to use these resources. Unless aquaculturists have a property interest in public areas (e.g., public waters, submerged lands) in which they wish to establish their operations, present South Carolina law will provide little if any protection.

We developed a set of criteria upon which a comprehensive leasing program could be structured for South Carolina. The leasing programs of ten states were evaluated by examining the following six criteria: types of properties subject to leasing (water column and/or submerged lands, for example); degree of exclusivity; rights granted under the lease (ownership of the stocks, protection from vandalism and theft, etc.); maximum size and duration; fee structures (fee simple, rents, royalties, etc.); performance criteria (including bonds); and penalties. Matrices were devised to allow for direct comparisons. Once the leasing provisions were identified, follow-up phone calls were placed to the leasing officials of the selected states to determine whether the leasing programs were indeed meeting the needs of the culturist, the public and the state. A prototype aquaculture leasing program was developed from this information.

RESULTS OF AN OYSTER-SHRIMP POND BICULTURE STUDY

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A study was undertaken to test the suitability of the American oyster (*Crassostrea virginica*) as an additional crop in an intensively managed shrimp pond at the Waddell Mariculture Center at Bluffton, SC.

In May of 1987, post-larvae of the Pacific white shrimp (*Penaeus vannamei*) were stocked in a 0.1 hectare pond at a density of 100/m^2. Natural oyster set was obtained during June on ridged plastic pipes, called French collectors, at the Clam Farm on the Folly River near Charleston. Thirteen hundred and fifty collectors (1350), holding approximately 27,000 oysters, were deployed in early July 1987. Shrimp were harvested in late October 1987, and oysters in spring 1988.

Both shrimp and oyster growth and survival were excellent, and Dermo (*Perkinsus marinus*) was conspicuously absent from the oysters. Oyster growth and mortality as a function of position in the pond, position on the collectors, and hydrographic parameters is discussed.

SUBTIDAL CULTIVATION OF THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*, IN FLORIDA UTILIZING A FLEXIBLE BELT SYSTEM

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American oyster culture is being tested in subtidal waters in the Indian River lagoon on the east-central coast of Florida. Seed oysters (>2500 micron) are placed in 2mm plastic mesh bags. An innovative belt design comprised of parallel polypropylene ropes, 2″ PVC spaces and closures, and plastic mesh bags is placed on the bottom using a dual-hulled tender vessel with a sub-surface deck and ramp.

Handling the oysters requires biweekly rotation of the bags to prevent biofouling and monthly culling and drying of oysters. The belt design facilitates handling of the oyster bags. Oysters are being tested for growth to market size using this method. When the oysters reach approximately 1.5″ (hold on a 1.25″ screen), they can alternatively be planted on .5″ plastic mesh elevated off the bottom. No protective covering is used for the final planting.

Using this method, oysters may grow to harvestable size in six to nine months.

A SEED-DEPENDENT BARATARIA BAY FISHERY: OYSTER ROULETTE?

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Oyster fishermen and their vessels (4 to 6) were monitored in Barataria Bay, Louisiana for three bedding seasons, 1982–85. Bay activities of *Thais haemostoma* and *Perkinsus marinus* on the seed leases were also monitored.

Seed abundance on the public reefs determined where the crews fished, the volume and number of seed loads freighted, vessel fuel consumption, and work days. The spring and summer of 1983 and 1984 had low snail and parasite activity. The yield ratio, combining 11 leases during the two years, was 1.24 sacks harvested for every sack bedded the previous fall (range 0.41–1.68). Spring and summer Bay conditions were significantly different in 1985 with higher snail and parasite activity. Four leases produced a combined yield ratio of 0.74 (range 0.66–0.86). Two other leases in 1985 produced ratios of 0.03 and 0.28 due to pollution (i.e., fear) and theft problems, respectively.

Daily labor and fuel needs while reharvesting showed less variation than while transporting the seed to the Bay the previous Fall. Total (bed + reharvest) diesel fuel consumption during the three seasons averaged 2.4 liters/sack harvested (l/s). Individual vessel consumption ranged from 1.5–4.6 l/s. An average of 69 sacks was harvested for each day of labor (bed + reharvest). Individual harvests ranged from 34–101 s/d. Relatively high fuel and labor inputs, periodic low yield ratios, and man-caused problems explain why development of the seed industry in the Bay is hindered.

FOOD VALUE OF TROPICAL MICROALGAE TO *MERCENARIA MERCENARIA* LARVAE; A PRELIMINARY STUDY

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Food value of microalgae, cultured under tropical conditions (temperature = 30°C, salinity = 30 ‰), were examined through

larval development in the bivalve *Mercenaria mercenaria* Linne, 1758. Preliminary results suggest that lengths of larvae fed with *Chaetoceros muelleri* Lemmermann (S/Chaet-2, SS-14), *Ellipsoidon* sp. (70–01) and *Nannochloris* sp. (Nanno2) in combinations of two, three or four, were as good as those fed with *Isochrysis* aff. *galbana* Green [Tahitian (T-ISO)].

High salinity and temperature tolerances, high lipid content, and high growth rate in seawater enriched with modified Guillard nutrients, make these microalgae suitable candidates as larval food for tropical molluses.

EFFECTS OF SEASONAL VARIATIONS OF CHLOROPHYLL-A AND TEMPERATURE ON HARD CLAM *(MERCENARIA MERCENARIA)* GROWTH

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To quantify the effects of variability of temperature and chlorophyll-a on growth of juvenile hard clams, weekly growth experiments were conducted in association with measurements of chl-a levels in a commercial land-based nursery. The remote field setting of the nursery required the use of fluorometry to monitor chl-a available to clams. Continuous measurements of in vivo fluorescence were calibrated by discrete chl-a extractions. Discrete chl-a analysis of size fractionated ambient water samples provided information on relative contribution of large (>14μm) and small (<14μm) phytoplankton to the total chl-a levels. Estimates of biomass increase were made from measurements of length, dry weight, and ash-free dry weight. Means of chl-a ranged from 5.5–2.3 μg chl-a/liter over the six week-long experiments; 60 to 70% of chl-a came from phytoplankton <14μm. Mean temperatures ranged from 19 to 22 degrees centrigrade. Preliminary results indicate that temperature affected growth more than chl-a levels.

FIELD NURSERY OF THE HARD CLAM *MERCENARIA MERCENARIA*, USING FLOATING UPWELLERS

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Floating upwellers are shown to be a viable alternative to land-based upwellers. Utilization of a field-based nursery has increased efficiency in a hard clam culture operation. Comparisons of growth and survival were made from a field upweller that uses natural phytoplankton to a land upweller that uses pumped natural phytoplankton or cultured microalgae. Field nursery growing of seed as small as 1000 μ, 500 μ and 300 μ, show this technique as a viable alternative to land-based nurseries.

BIVALVE DISTRIBUTION AND MORPHOLOGY

WINTER BURIAL OF NORTHERN BAY SCALLOPS, ARGOPECTEN IRRADIANS IRRADIANS

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This study investigated the progression and prevalence of bay scallop mortality due to burial by shifting sediments. In December 1987, groups of 20–25 mm, individually marked scallops were planted in Northwest Creek, East Hampton, New York, then monitored through March 1988. Ten days after release, 14% of all observed scallops were completely buried and 27% were partially buried. Burial appeared to be slightly more prevalent in muddy than sandy areas. Depth of interment often fluctuated; several individuals which had become wholly buried were later found on the sediment surface.

Laboratory studies examined survival rates of scallops in various states of burial. All individuals covered with 1 or 3 cm of sand or mud suffocated within one week; virtually all partially-buried scallops survived for at least one month. Movements which resulted in scallops becoming unburied increased noticeably when water temperatures rose from 3°C to between 7–8°C.

Burial of scallops by shifting sediments, therefore, is likely to

be most prevalent when the activity level of individuals is reduced at low water temperatures. This phenomenon is seen as a potentially significant cause of bay scallop mortality in winter which should be considered when implementing reseeding programs.

This work is the result of research sponsored by the New York Sea Grant Institute, under Grant # NA86AA-D-56-045.

MONTHLY CHANGE OF BEACH PROFILE AND THE DISTRIBUTION OF SANDY BEACH BIVALVES AT THE HASAKI OCEANOGRAPHICAL RESEARCH FACILITY

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It is difficult to study the ecology of sandy beach bivalves in the surf zone. In this region, much sediment movement takes place, particularly during rough sea and most of the organisms are influenced. We collaborate with the Port and Harbour Research Institute on the study of the beach morphology and the ecology of sandy beach organisms at the Hasaki Oceanographical Research Facility (HORF) in Ibaraki prefecture. HORF is built on the surf zone, and has 392m length and 7.5m height platform. It is possible to carry out field observation even in rough sea conditions.

From November 1986 to January 1988, beach profile were measured with lead and sediment were sampled with the Smith-McIntyre grab along the platform at a monthly intervals. These samples were then separated, analyzed, and sorted accordingly. The number and shell length of two species of bivalves (*Meretrix lamarckii, Gomphina melanaegis*), which are commercially important, were then recorded.

Hasaki beach is a typical bar-type and beach profile fluctuated even on calm sea. These two species tended to distribute on the offshore side of bar. After severe sea conditions, the profile and the pattern of bivalve distribution changed drastically. Heavy storms were observed in February, June, September. Usually, in the eroded region, substratum became coarse and the bivalves were fewer. However, after a storm in June, the youngs of *Gomphina* (approximately 20mm shell length) were accumulated at the lowest point of trough. It was speculated that the interaction between wave height (suspending force) and size of the bivalves (burrowing behavior) related to the distribution pattern.

PORES IN THE SHELLS OF *CORBICULA FLUMINEA*

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Shells of *Corbicula fluminea* collected from the Delaware and Maurice Rivers, New Jersey, contain small (4–10 μm in diameter) pores near the umbo which contain thin processes of the mantle epithelium. Many, but not all, of the pores were bifurcated and traversed the entire thickness of the shell in regions where the periostracum and outer complex crossed lamellar shell layer were eroded away. Pore walls were not composed of the cone complex crossed lamellar microstructure of the inner layer, but were instead formed of columnar prisms. Shell pores, and presumably the thin mantle processes associated with them, were more numerous and covered a larger percentage of the inner surface of the inner layer in shells collected from a site in the tidal freshwater portion of the Maurice River (where there was extensive erosion/dissolution of the outer surface of the shells near the umbo) than from either of two other sites, one in each of the Delaware and Maurice Rivers (where there was considerably less shell erosion/dissolution). A possible role in prevention of shell erosion by secretions through the mantle processes to the outer shell surface is presented.

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BIVALVE REPRODUCTION AND PHYSIOLOGY

THE REPRODUCTIVE CYCLE OF THE HARD CLAM, *MERCENARIA MERCENARIA*, IN WASSAW SOUND, GEORGIA

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The reproductive cycle of a *Mercenaria mercenaria* population from Wassaw Sound, Georgia was analyzed from December 1983–July 1986. Qualitative (staging criteria and gonad indices) and quantitative (*Female:* Oocyte diameter; percent eggs; number of eggs; percent gonad. *Male:* Percent spermatozoa; percent spermatogenic cells; percent gonad) data was compiled monthly from histological preparations, and used in the assessment of reproductive condition.

A continuous gametogenic cycle was indicated throughout the study period. Sex ratios were 1:1. A synchronized polymodal breeding pattern was evident, with three (Spring, Fall, Winter) annual spawning peaks. Temporal differences in reproductive output were detected, with 1985 levels apparently greater than those of 1984. The results of this study are discussed in the light of previous reports on hard clam reproduction from the eastern United States.

SEASONAL CHANGES OF LIPIDS AND FATTY ACIDS IN OYSTERS

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It is accepted that fatty acid composition of an animal, especially the neutral lipid in deposit fat, is dictated by the products of the animal's metabolic activity and by the components of its dietary lipids. It has been shown in our laboratory that the adult oyster of *Crassostrea virginica* has limited capacity to elongate dietary fatty acids (e.g., 18:2ω6 and 18:3ω3), and no desaturation of dietary fatty acids was observed. The fatty acids, 20:5ω3 and 22:6ω3, are considered essential for the oyster. To determine whether there is a balance between exogeneous (dietary) and endogeneous lipids and fatty acids in oysters and if the balance changes seasonally, the distribution of lipid and fatty acids in different tissues of oysters maintained in estuarine water is being investigated. Preliminary results demonstrate that there were marked seasonal fluctuations in the content of total lipid in mantle plus gill, heart and adductor muscle, but not in the viseral mass. Proportions of the fatty acid groups remained similar in adductor muscle and viseral mass. The weight percent of total omega-3 polyunsaturated fatty acids in mantle plus gill declined gradually from January to the lowest in June and increased after July. The increase of omega-3 polyunsaturated fatty acids in mantle plus gill appears to correlate with the weight percent of omega-3 fatty acids in the diet. The seasonal variations of lipid content and weight percent of omega-3 fatty acids may relate to the oyster reproduction. It is interesting to find that consistently the heart has the highest amount of lipid during each season.

AN IMMUNOLOGIC TECHNIQUE FOR QUANTITATING OYSTER EGGS

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A quantitative gonadal index is not generally available in bivalves because a direct measure of gonadal weight is usually difficult. Accordingly, an immunologic technique was developed for quantitatively monitoring gonadal maturation in *Crassostrea virginica*. Gonads from female ripe oysters were removed, eggs stripped into phosphate buffered saline (0.15 M NaCl, pH 7.3) (PBS II) and sieved over 100 μm mesh to separate eggs from cellular debris. The preparation was layered onto a discontinuous gradient of 20%-, 30%-, 40%-, and 50% Percoll and centrifuged at 765 g at 10°C, for 20 min. The purified egg fraction was concentrated at a density of 1.098 g/ml, washed twice in PBS II, sonicated for 2 min using an ultrasonicator (30 watt, 20 KH), and the protein adjusted to approximately 100 μg/ml.

The preparation was mixed with equal parts of Freunds complete adjuvant for initial injection and equal parts of Freunds incomplete adjuvant thereafter. Albino New Zealand rabbits (NZ-30) received 1 ml injections on a biweekly basis for 8 weeks, at which time the immune status was assessed by passive hemagglutination using bovine erythrocytes coated with the oyster egg material. Rabbit immunoglobulin (IgG) was extracted by ammonium sulfate precipitation. Goat anti-rabbit alkaline phosphate labeled conjugates were used in a sandwich enzyme linked immunosorbent assay (ELISA) to quantify oyster egg proteins. The rabbit anti-oyster gonad IgG (1.0 μg/ml) detected oyster egg proteins within a range of 1 to 7 μg/ml.

CRAWFISH

OVERVIEW OF INTERNATIONAL AND DOMESTIC FRESHWATER CRAWFISH PRODUCTION

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Freshwater crawfishes are the dominant macrobenthic inverterbrates in many temperate aquatic environments. Over 400 species belong to three families: Astacidae (Europe and North America), Cambaridae (eastern Asia and North America and Europe and Africa-introduced), and Parastacidae (Austro-New Guinea region, southern South America, and Madagascar). Important commercial/recreational genera are *Astacus*, *Cherax*, *Euastacus*, *Orconected*, *Pacifastacus*, and *Procambarus*.

Estimated annual production (1988) is at least 60,000, 4,000, 2,000, and 500 metric tons in the USA, Europe, Asia, and Australia, respectively. Several hundred thousand hatchling and yearling crawfishes are produced annually in Europe and Australia. *Procambarus clarkii*, the red swamp crawfish, accounts for 90% of all crawfish harvested. It is native to the southern USA and northeastern Mexico. It is now firmly established throughout the USA and perpetuating populations are present in the Caribbean, Central America, South America, Hawaii, Japan, Taiwan, mainland China, Africa, Cyprus, and Europe. The red swamp crawfish is cultured in 64,000+ ha of earthen ponds, often in some rotation with rice, in the southern USA.

North American species have been introduced into Europe to replace native species decimated by the fungal disease, *Aphanomyces astaci*. These species are highly resistant to the disease and are potential vectors for it. They should, therefore be excluded from contact with parastacid crawfishes which have no resistance162 to the malady.

COMMERCIAL CRAWFISH CULTIVATION PRACTICES

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In Louisiana, commercial crawfish fishermen harvest 100 million pounds of crawfish annually with a $65 million value to the industry. Catch is dependent on river stages and weather conditions but generally 60% is caught in ponds and 40% in the natural fishery of the Atchafalaya Basin. Ponds have stabilized the industry and expanded the harvest period from 3 months to 8 months.

Crawfish aquaculture is successful because of the low investment required, low risks, profits and ability to incorporate crawfish culture into ongoing agricultural practices. Crawfish can be grown as a single crop in permanent ponds, double cropped with rice or milo or grown in combination with rice and soybeans. Total crawfish pond acreage in Louisiana is 135,000 acres.

Pond construction techniques, water demands and various management strategies are discussed as related to total investment and production per acre.

FORAGE AND FEEDING SYSTEMS FOR COMMERCIAL CRAWFISH CULTURE

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Crawfish are not typically fed prepared rations, but organic substrates supporting rich microbial communities are provided for them to forage upon various components of a detrital food web. Crawfish readily accept a prepared feed, but the economic feasibility of intensive feeding has not compared favorably with the forage based system.

Farmers traditionally relied upon native vegetation such as alligatorweed *(Alternanthera philoxeroides)*, smartweed *(Polygonum* spp.), water primrose *(Ludwigia* spp.), and other aquatic or semi-aquatic plants to provide the organic substrate to support the detrital system. These are undependable and difficult to manage, however, and agronomic plants have recently gained popularity.

Agronomic plants provide the opportunity to increase system intensity by double cropping with crawfish. Crawfish have been harvested as an incidental crop from Louisiana rice fields for many years, and rice remains the mainstay crawfish forage. Grain sorghum has also recently been identified as a viable double cropping alternative to rice.

The recurring problem of forage substrate depletion has led full circle to a recently renewed interest in feeding crawfish a prepared ration. Substantial research is planned to address nutritional requirements of crawfish and to assess the feasibility of supplemental and/or intensive feeding practices and their potential impacts upon crawfish production technology.

OVERVIEW OF HARVEST TECHNOLOGY USED IN COMMERCIAL CRAWFISH CULTURE

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The high cost of harvesting crawfish has been identified as the most important production impediment to expansion and increased

profitability of the crawfish culture industry. Crawfish harvesting practices are inefficient and labor intensive. Harvest expenses normally range from $120 to $1,200 per acre with the major expenses being labor to bait and empty traps (24% of annual operating expenses), bait (48%), sacks (1%) and fuel (9%).

Crawfish are commercially harvested 60 to 180 days annually (mid-November through May) with small, wire traps (3.3-ft L x 1.3-ft diameter) constructed from ¾-in hexagonal mesh wire. Traps are baited with fish, manufactured bait, or a combination of fish and manufactured bait. Crawfish catch is maximized when 30 to 40 traps per acre are used. Traps are lifted and emptied with the aid of several different types of harvesting machinery. The trap design, type and quantity of bait used, trap soak time, climate, molting pattern, and water quality significantly influence crawfish harvest efficiency.

Efficient methods for harvesting crawfish must be developed to increase crawfish production efficiency and profitability for producers. Ideally, crawfish should be harvested with minimal use of traps, bait and labor. Mechanical harvesters are being developed that will eliminate the need for baits and traps. Water current is being investigated as a means of stimulating crawfish movement to areas in the crawfish ponds where the crawfish are harvested more effectively with unbaited nets or traps.

DIVERSIFICATION OF CRAWFISH MANAGEMENT SCHEDULE

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Commercial crawfish farmers typically manage culture ponds for a spring harvest (Apr–May). Some crawfish operations have started to extend the harvest into summer to take advantage of lessened competition among producers and a more favorable price structure. Six 0.02-ha ponds were used to evaluate crawfish production and standing crop biomass of forage in ponds managed on a standard (control) and extended schedule. Three control ponds were stocked each with 7.3 kg of adult crawfish in May, drained in June, planted with rice in July and reflooded again in October. These ponds were harvested with baited traps the following spring after water temperatures reached 13°C. The extended management schedule followed the same sequence of events except the management activities were delayed approximately one month. In the first year of production (1986–87), ponds under the standard management schedule had approximately 2 times the amount of forage as those ponds managed under the extended schedule. Crawfish production, however, was similar in the two management strategies; harvests averaged 991 kg/ha (810-1239) and 853 kg/ha (440-1210) in the standard and extended managed ponds, respectively. The overall standing crop biomass of rice and volunteer plants in ponds was higher during the second production year (1987–88) and no difference was detected between treatments. A detailed comparison of the upcoming second year's crawfish production will be presented with a discussion of management recommendations.

OVERVIEW OF SOFT-SHELL CRAWFISH RESEARCH AND TECHNOLOGY

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Although soft crawfish *(Procambarus clarkii)* have been consumed incidentally in Louisiana for many years, commercial-scale production has only recently materialized. Production depends on obtaining immature crawfish during the crawfish season. Soft crawfish are produced by holding and feeding immature hard crawfish in high densities until they molt (ecdysis). Most edible-size intermolt (hard-shelled) crawfish will molt within a 40-day period when properly fed.

Several types of culture systems are possible, but all have common requirements: Culture tanks contain shallow water (2.0–2.5 cm) of good quality. A constant aerated water flow is required. Density ranges from 4–4.5 kg crawfish/m^2. A water temperature of 20–30°C is maintained.

Water quality standards suitable for producing soft crawfish include: pH of 6.0–9.0, calcium hardness and total alkalinity do not have to exceed 5 mg/l, and oxygen above 3 mg/l. Total ammonia (NH_3 + NH_4) should not exceed 0.5 ppm, nitrite (NO_2) 0.3 ppm, and iron 0.2 ppm.

Hard crawfish must not be mishandled during trapping and transporting, or mortality will be excessive. Crawfish are acclimated in the culture trays over a 24-hour period. Crawfish approaching the molt phase (premolt) show distinct color changes. Premolt crawfish are transferred to a molting tray. The daily molting rate of the total population averages 2–3% under proper management.

Fresh soft crawfish are placed in plastic bags, covered with water, and frozen. Processing is done by the purchaser. Minimum processing require removal of the two gastroliths behind the eyestalks, leaving 93% edible product. Removal of carapace and

organs (called crawfish fat) is sometimes practiced, leaving 72% edible product.

CRAWFISH PROCESSING

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Louisiana leads the nation in crawfish production and processing facilities. The state currently licenses more than 70 processing plants. Most processing plants produced peeled and deveined tail meat that is sold fresh or frozen. Two distinct species are processed jointly without regard to separation since no appreciable differences are noted in the finished packaged product. Live crawfish are processed immediately or are stored at 40°F until processing. Commonly, crawfish are graded according to size prior to processing. Large mature crawfish are separated for the whole cooked or live market sales. Processing involves washing, blanching, hand peeling, packaging, chilling and storage. Blanch times must be carefully controlled. Undercooking will not destroy proteolytic enzymes and may result in a mushy textured product. Overcooking will significantly slow the hand picking operation and create complaints by the workers. A simple in-plant cooking test that can be routinely performed by employees has been developed by LSU. Removal of the crawfish meat is highly labor intensive and is considered to be an area of major sanitation concern. Careless employee practices here can lead to serious bacterial contamination. The finished meat is packaged in flexible pouches. Hepatopancreas, erroneously called "fat" by local consumers, is an important component of the fresh meat. This yellow-orange, semi-liquid tissue can equate up to 13% of the final package weight although the average is about 8.5%. Because it is unstable during freezer storage, it should be removed by rinsing prior to packaging. The shelf-life of fresh meat is about 8 days and the shelf-life of frozen, vacuum meat is 6–8 months. Crawfish meat that is intended for freezing has special recommended processing procedures. Other crawfish products such as whole boiled and soft-shell are becoming more important in the overall marketing programs.

LOUISIANA CRAWFISH PRODUCTS IN DOMESTIC AND INTERNATIONAL MARKETS

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The nation's largest crustacean aquaculture industry is centered in Louisiana. With over 130,000 acres devoted to crawfish farming businesses, the 1987 production reached 72 million pounds. Additional supply from natural areas often depresses priced received. Although marketing efforts have been accelerated and become better organized, plentiful supplies maintain pressure on prices. The major market remains south Louisiana. Failure of this market to expand in the depressed petroleum based economy has lead to more valued added processing. Approximately eighty processing/marketing companies now prepare products for food service and at-home consumption. Recent research indicated a yet untapped market within Louisiana remains in the at-home segment. This is significant because of the general lack of large crawfish meat purchases by major food service companies. Two 1987 market developments may again heighten interest in overall crawfish products. The decline of the dollar against foreign currencies and supply contraints in Turkey provided a market opportunity in Europe. Louisiana exports to Europe are delineated and discussed as to potential. Soft shell crawfish supply and markets represent the second prospect. These expansions are essential in order to maintain growth anticipated in ponds and yield per acre.

LOUISIANA OYSTER INDUSTRY

ADMINISTERING TO THE LOUISIANA OYSTER FISHERIES

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Louisiana's oyster production has varied slightly over the years dating back to the early 1800's. However, during the last 5 years it has increased slightly now averaging in the neighborhood of 12.5 million pounds. The management of these fisheries has been entrusted to the Louisiana Department of Wildlife and Fisheries. The productive areas in coastal Louisiana are divided between those which can be leased by Louisiana residents for private oyster farming, and those areas designated as "Public Oyster Seed Grounds" available for both seed oyster production and direct commercial harvest.

The administration of the private leased areas consist of fielding survey crews to physically place and keep track of the more than 270,000 acres presently under lease from the state.

The administration and management of the "Public Oyster Seed Grounds" requires the sampling of these grounds to deter-

mine available supplies on different portions of these grounds and the size distribution of these oysters. Spat catch sampling stations, meter square samples along with the environmental samples (i.e. salinity, temperature) are all used to formulate a structured season on these public grounds for the fishing year. Fishing pressure is also monitored once the season has begun and allowances are made to the season structure to compensate for the pressure.

There are additional administrative concerns associated with controlled freshwater introduction to control salinities, oyster mortalities and damages to the oyster reefs, health closures, and laws pertaining to the harvesting of the resource.

MANAGING PUBLIC OYSTER REEFS: TEXAS EXPERIENCE

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In August 1987, the Texas Parks and Wildlife Commission ordered the 1987–1988 oyster season closed because sampling data indicated that market-sized oysters were too sparse for harvesting without risking depleting public reefs. Oystermen, however, believed that there were ample oysters for harvesting and that oystering would cease before stocks were endangered. A group of oyster dealers and fishermen filed suit against the Texas Parks and Wildlife Department (TPWD) in December 1987. The judge ruled for immediate opening of the season—thus creating an adversarial position between oystermen and TPWD.

The Texas legislature mandated that TPWD develop an oyster management plan that would consider socio-economic impacts as well as biology and law enforcement. Such a plan has not been completed. An effective plan should have input from the oyster industry and from knowledgeable scientists from other agencies and institutions. We suggest that the plan include the encouragement of private oyster leasing in appropriate areas; the involvement of fishermen and dealers in such management options as bag and size limits, reduced harvest times and flexible seasons along the Texas coast; and TPWD catch data should be reported in terms that fishermen can understand (such as sacks per hour). Furthermore, a commercial dredge rather than a smaller sample dredge should be used in assessing oyster density.

Because of increased fishing and oyster population fluctuations due to climatic conditions, studies of the origin, dispersal and setting of oyster larvae, oyster survival and impact of predation and diseases are needed.

OYSTER HATCHERIES ON THE GULF COAST: HISTORY, CURRENT TECHNOLOGY AND FUTURE PROMISE

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The history of oyster hatchery development in the Gulf of Mexico will be presented. The brown water culture method will be described and its increased usage discussed. Current practices for setting of eyed larvae will be reviewed. Previously unreported results from the GCRL hatchery relating to setting performance of larvae, loss of larvae to setting, and mortality of spat will be presented. A hypothetical system for setting of larvae on shell from a commercial hatchery will be presented.

OIL AND OYSTER INDUSTRY CONFLICTS IN COASTAL LOUISIANA

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The juxtaposition of the oil and oyster industries in coastal Louisiana has led to inevitable conflicts. Chief among these problems are the sedimentation and burial of oysters due to dredging and other operations. (Oil spills are relatively rare events.) A system of compensation has evolved in which oystermen, who lease the waterbottoms from the State of Louisiana, are paid for damages due to oil and gas activities. Methodologies for the assessment of damage, the rights of oystermen in relation to the oil industry, and major legal issues are reviewed.

THE LOUISIANA OYSTER INDUSTRY: ECONOMIC STATUS AND EXPANSION PROSPECTS

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As the nation's largest marine fisheries producer, Louisiana achieves its rank through diversity. Crustaceans, mollusks, and finfish businesses are numerous and often specialized by species.

Within the state's oyster industry significant diversity exists in a diminishing coastal area. The authors delineate the production of oysters from public grounds and private leases. Trends in landings, prices, and value demonstrate the importance of the industry in Louisiana and U.S. oyster industries. Tabulation of industry licensees suggests the employment potential may have peaked. A linkage between publicly owned seed grounds and production on private leases was analyzed. The value added aspect of the industry was analyzed via processing data.

The future impact of the oyster industry hinges on improved value added figures. As the state's coastal area diminishes, oyster producers will be implementing more forward looking practices. These include seed production, depuration, and mechanical grading. Also state management agencies may be able to mitigate coastal erosion in the state by altering leasing practices. To this extent, the oyster industry can help the state as well as the state aiding the oyster industry.

AN OYSTER FARMER'S PERSPECTIVE TO THE PAST, THE PRESENT, AND THE FUTURE OF THE LOUISIANA OYSTER INDUSTRY

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The Louisiana oyster industry has a long history dating back to the mid 1800's, and as the annual production figures will indicate it's had its ups and downs. Present production ranks it first nationally; however, there are limited individual production, due to environmental condition, increases in the number of fishermen due to a declining Louisiana oil economy, and increasing health restrictions, and several other problems.

There will have to be changes made to the way the industry does business and the way the "Public Seed Grounds" are managed to make segments of this industry economically solvent.

SHELLFISH SANITATION STUDIES IN LOUISIANA

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Shellfish sanitation is based on allowable numbers of fecal coliform "indicator" bacteria in shellfish and growing waters. However studies of the relationships between enteric viruses and bacterial indices in Louisiana oysters and waters indicated that viruses do not always correlate with the fecal coliform indicator system.

The indicator system was further questioned when Louisiana oysters harvested from approved growing waters in summer months contained excessively high levels of "fecal coliforms". These proved to be non *E. coli* fecal coliforms (mainly *Klebsiella* species). They outnumbered *E. coli* 1000 to 1 in oysters in summer months, but were apparently not of sewage origin and were non-pathogenic. This problem resulted in a one year interim *E. coli* rather than fecal coliform guideline in oyster meats. However the standard 10 day method for the enumeration of *E. coli* in shellfish was inappropriate for perishable shellstock oysters. A study of several rapid methods for *E. coli* in Louisiana oysters proved that a 48 hour fluorogenic assay using MUG in EC media was very sensitive for *E. coli* in oysters with high fecal coliform: *E. coli* ratios.

The concern with non sewage-related marine *Vibrio* pathogens in Louisiana oysters and the large percentage of areas closed for shellfishing due to sewage pollution resulted in studies using ionizing radiation to eliminate *Vibrios* and reduce indicators from shellstock oysters. Doses of 100,000 rads of gamma irradiation reduced all *Vibrio* pathogens to undetectable levels, but were not lethal to shellstock oysters (LD_{50} = 250,000 rads). Sensory evaluation of radiation processed raw oysters showed no significant differences from the non-irradiated controls.

Studies to evaluate the effectiveness of commercial depuration to remove indicators and pathogens from live shellstock oysters are planned.

A national collaborative study on the relationships between indicators, enteric pathogens and health risk in shellfish and waters is being developed.

POSTER SESSION

OVERWINTERING HARD CLAMS, *MERCENARIA MERCENARIA*, IN SOUTH CAROLINA SHRIMP PONDS

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The pond culture of penaeid shrimp is showing increasing popularity in coastal South Carolina. However, due to the temperate climate in South Carolina, the pond culture of shrimp is restricted to the warm summer months. Northeastern clam farmers have shown an interest in leasing southern shrimp ponds for the nursery culture of hard clam seed during the off season or winter months.

This would benefit the clam farmer by eliminating the need for a winter nursery system and by suppling them with field planting size seed in the spring. The shrimp farmer would profit from the additional income.

Studies were performed during the winter months of 1985, 1986, and 1987 in vacated shrimp ponds to assess the growth and survival of overwintered hard clams. Several seed sizes, stocking densities, and stock sources were tested. The ponds were stocked in November, after shrimp harvest, and sampled monthly through April or May. Results indicate that South Carolina shrimp ponds work well as winter nurseries for hard clams. Small seed (1.4 mm) had a size increase of almost 300% over a four month period with little mortality. Large seed (7.5 mm) doubled in size over the same time period, again with little mortality. In this test, growth was independent of density. In another study, density appeared to have an affect on 4.5 mm clams stocked at densities of 200 and 2,000/ft^2. Low density clams increased in size over 200% during a six month period, while the clams stocked at 2,000/ft^2 had a size increase of only 100%. No significant difference in survival was noted.

AN SEM STUDY OF HAPLOSPORIDAN SPORES FROM *TEREDO NAVALIS*

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Shipworms infected with *Haplosporidium* sp. were collected from Wachapreague, Virginia in October, 1987. Sections of gill tissue were dissected and either preserved immediately in glutaraldehyde or smeared onto coverglasses prior to fixation. In addition, spores were obtained by allowing pieces of infected tissue to decay in a beaker of seawater for approximately 7 days until only spores remained. These spores were preserved in glutaraldehyde and adhered to poly-l-lysine coated coverglasses. All preparations were post-fixed in osmium tetroxide, critical point dried and coated with gold/palladium by vacuum evaporation prior to examination with the scanning electron microscope. Surface ornamentation of the spore was unique in having 4 projections of the epispore membrane—two opposing lateral projections, one abopercular projection, and one eccentrically situated opercular projection opposite the opercular hinge. Epispore projections were 10 to 30 μm in length. The epispore membrane appeared as a thin, loose covering and was often partially lysed and pulled away from the spore as if being shed. Many spores were observed with no epispore membrane or projections. Spore ornamentation has been proposed as a diagnostic character in the Haplosporida, but absence of ornamentation should be viewed with caution if the epispore membrane is shed as suggested by these results.

A VIDEO DIGITIZING TECHNIQUE FOR COUNTING JUVENILE QUEEN CONCH *(STROMBUS GIGAS)*

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In all phases of hatchery operation, monitoring stock abundance is vital to assessing levels of mortality, and for planning purposes. A technique was developed for counting large numbers of juvenile Queen conch (*Strombus gigas*) at the Caicos Conch Farm, a commercial hatchery and grow-out operation in the Turks and Caicos Islands, BWI. A high resolution video camera, mounted on an X-Y axis movable trolley, viewed batches of 1,000 to 20,000 post larval conch (shell height 1.2 mm to 12.0 mm) resting in a water bath beneath the camera. Batches of conch were pre-sieved to a uniform size class prior to being counted. Through a series of "snap-shots", a microcomputer-driven image analyzer, interfaced with the camera, measured total plan view surface area of the animals. Numbers of conch were rapidly estimated (± 10%) based on the mean individual surface area for the size class. Benefits of the system are speed and lack of human bias in estimating counts.

DO MARINE BIVALVES CARRY UNUSUALLY HIGH LOADS OF DELETERIOUS MUTATIONS?

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There are several indirect lines of evidence which suggest that marine bivalves harbor a relatively high load of deleterious recessive mutations (genetic load). This could be due either to a higher mutation rate in marine bivalves relative to other taxa or to a greater ability of marine bivalves to tolerate mutations. An estimate of the degree of mutational load might settle several unresolved issues in bivalve genetics, such as (1) the relationship between heterozygosity and fitness related traits (such as growth) commonly reported in marine bivalves, (2) the frequent occurrence of heterozygote deficiencies (compared to Hardy-Weinberg expectations) in marine bivalve populations, coupled with unusually high levels of genic polymorphism, (3) the decrease in heterozygote deficiencies with increased age, (4) the occurrence of allozyme null activity alleles at unusually high frequencies in these species, and (5) whether bivalves exhibit high levels of inbreeding depression.

Our approach to the question of mutational load in marine bivalves has been to compare species of differing life histories and look for evidence that mutational load is correlated with life history pattern. The goal of our research is to produce a general model from which we can test specific hypotheses experimentally. The implications of increased mutational loads for applied breeding programs as well as for basic genetic processes (such as rates of mutation and gene substitution) will be discussed.

NOCARDIOSIS OF ADULT PACIFIC OYSTERS, *CRASSOSTREA GIGAS*

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Focal necrosis of adult Pacific oysters (*Crassostrea gigas*) has been reported to coincide with recurrent mid to late summer mortalities in Matsushima Bay, Japan. The disease, now designated Pacific oyster nocardiosis (PON), has also been observed among Pacific oysters in the state of Washington, U.S.A. where it is believed to cause significant mortalities during mid summer to early fall. The nature and significance of the disease to oyster populations is still poorly understood. We have examined oysters from 10 sites in Washington and three sites in British Columbia, Canada in an effort to better characterize the etiology, pathogenesis and distribution of PON.

The principal lesion is composed of host inflammatory cells (amoebocytes) surrounding colonies of gram-positive, acid-fast, beaded and branched actinomycete-like bacteria. Lesions are primarily found within oyster vesicular connective tissue cells surrounding the gut and digestive diverticulae. A bacterium with the same tinctorial and morphological properties noted above has been isolated from diseased oysters collected in several of the sample sites. Thin-layer and gas liquid chromatographic analyses of extracted bacterial cell wall mycolic acids (lipids) indicate that the bacteria belong to the genus *Nocardia*.

Injection of the isolated bacterial cultures into the branchial vein of Pacific oysters reproduces the same gross and histological pathology observed in naturally infected animals. The same bacterium has been reisolated from challenged oysters indicating that the nocardial bacterium is the etiological agent of PON. Cohabitation experiments in which diseased oysters are incubated with uninfected animals indicate that the disease is not easily transmitted via the water. Further experiments regarding the taxonomic placement of the pathogen and transmission of the disease are currently in progress.

PENETRATION OF CULTCH MASS BY EYED LARVAE OF *CRASSOSTREA VIRGINICA*

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During remote setting, eyed larvae of the American oyster, *Crassostrea virginica*, are added to a tank holding cultch (50 to 100 bushels of oyster shell bagged in 13″ lay-flat Vexar) in filtered, aerated seawater. Larger cultch containers are more desirable if eyed larvae can penetrate larger, tightly packed masses of shell. To observe whether natural sets of *C. virginica* can penetrate large cultch masses, cages (1.5 × 0.9 × 0.9 m) of cultch were placed off New Point Comfort, Mobjack Bay, in July 1987. All cage sides were covered with oysters when recovered in November 1987. More spat were found on the exterior than the interior. Few spat were found deeper than 15 cm in the cultch mass. The ability of eyed larvae to penetrate tightly packed cultch held in containers with restricted access was tested. PVC pipes (10 cm diameter, 90 cm length) were filled with six shell bags of 15 cm length. Aeration was provided to each test chamber but not the controls. Chambers were sealed leaving only the ends available for larval access and placed horizontally in a 50 l tank for a setting period of 96 hours. Higher numbers of spat per shell were found in chambers with aeration. The end bags in all chambers had more spat per shell than interior bags. Eyed larvae penetrated to a depth of 15 cm large, tightly packed cultch masses and cultch with restricted access. Aeration enhanced the set on cultch. Aeration should be provided to enhance setting in large cultch masses.

A PATHOLOGY POTPOURRI FROM THE NOAA MUSSEL WATCH PROGRAM

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Histological examination of bivalve tissues collected for the Mussel Watch Program has resulted in a variety of significant pathological findings. These findings include incidences of reduced fecundity in *Mytilus edulis*, probably as a result of poor water quality; inhibition of gonad follicle development in *Mytilus edulis* and *Crassostrea virginica* by the presence of trematodes in the tissues; the occurrence of hemic neoplasms in *Mytilus edulis* from Long Island Sound and Puget Sound, and in *Ostrea sandwichensis* from Honolulu Harbor; the occurrence of *Steinhausia mytilovum* in *Mytilus edulis* from Marina del Rey, California; and the occurrence of the oyster pathogen, *Haplosporidium nelsoni* (MSX) at sites as far south as the St. Johns River in Florida.

The hemic neoplasm in the mussel from Long Island Sound is believed to be the first reported neoplasm of that type in mussels from the east coast of the United States. Likewise, the neoplasm in *O. sandwichensis* is the first of its type reported in that species, as well as the first from the Hawaiian Islands. *Steinhausia mytilovum* has never been reported from the west coast of the United States and occurs only infrequently along the east coast. The St. Johns River is believed to be the southern-most extension of the range of MSX.

GENETIC DIFFERENTIATION AMONG POPULATIONS OF THE BAY MUSSEL, *MYTILUS EDULIS* FROM POPULATIONS ALONG THE COAST OF CALIFORNIA

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Recent allozyme surveys of *Mytilus edulis* populations have suggested that certain populations are actually complexes of morphologically similar subspecies or species. For example, electrophoresis has revealed that in areas of the British Isles *Mytilus* populations actually consist of two species: *M. edulis* and *M. galloprovincialis*. Also, researchers have suggested that *Mytilus* populations in the Atlantic Canadian Provinces and areas of northern Canada may actually consist of two species. A study of the population genetics of the blue mussel, *Mytilus edulis*, from eight populations along the coast of California revealed significant genetic differentiation among populations. Analysis of five polymorphic enzyme loci (aminopeptidase, glucose-6-phosphate dehydrogenase, leucine aminopeptidase, octopine dehydrogenase and phosphoglucomutase) revealed the populations to be differentiated into two groups, a southern group (populations south of Mendocino) and a northern group (populations north of Mendocino). Allele frequency differences between these two groups indicate that these populations are genetically quite different. The data presented in this study suggest that Pacific coast *Mytilus edulis* may actually be a complex of two species or a species represented by populations which differ in their multilocus genotypes.

ULTRASTRUCTURAL STUDIES OF MSX *(HAPLOSPORIDIUM NELSONI) AND OYSTER HEMOCYTE INTERACTIONS*

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Interactions between the protozoan parasite MSX (*Haplosporidium nelsoni*) and hemocytes from its oyster host (*Crassostrea virginica*) were examined by transmission and scanning electron microscopy. In the gill epithelium, granular hemocytes were often found in close proximity to the parasite with plasma membranes in tight apposition. Frequently, there was evidence of cytopathological changes in the hemocytes, including extensive vacuolization and leaching of the cytoplasmic matrix. Parasites occasionally appeared to be degenerating, with pycnotic nuclei, leaching of cytoplasmic matrix, and deterioration of plasma membrane; but, this condition was not necessarily associated with the presence of hemocytes and there was no clear evidence of phagocytosis. Many hemocytes did have large digestive lamellae suggesting involvement in catabolism of damaged host tissue, parasite waste products, or both. Phagocytosis of entire MSX plasmodia, parasite fragments, and other hemocytes was seen in blood samples from some oysters. The phagocytic cells were agranular and characterized by the presence digestive lamellae, abundant smooth endoplasmic reticulum, and large phagosomes containing ingested material. Scanning electron micrographs of *in vitro* samples showed hemocytes with broad ectoplasmic extensions spread over parasite surfaces.

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GENETIC DRIFT AND EFFECTIVE POPULATION SIZES IN COMMERCIAL STOCKS OF THE PACIFIC OYSTER, *CRASSOSTREA GIGAS*, ON THE U.S. WEST COAST

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Culture of the Pacific oyster *Crassostrea gigas* along the west coast of the United States relies almost exclusively on seed produced by a few major commercial hatcheries. Because this introduced species reproduces naturally in only a few localities, commercial stocks have in recent years been maintained in isolation from natural stocks. While such isolation makes possible domestication and genetic improvement, it necessitates the careful management of these captive gene pools. Improper broodstock management and ill-conceived breeding programs result in inbreeding, reductions in genetic diversity, and declines in performance.

Using allozyme analysis we have scored individual differences at 14 polymorphic enzymes in samples of natural set from Debob Bay, Wa., and in samples of third generation hatchery stocks derived from such natural set and reared on commercial growout beds in Willapa Bay, Wa., and Humboldt Bay, Ca. Hatchery stocks differ markedly from the naturally recruiting population at many loci. Assuming that the Dabob Bay sample represents the population from which the commercial stocks were derived, we calculate that the genetically effective population sizes of the Willapa and Humboldt stocks are only 42 ± 15 and 8 ± 2, respectively. Continued use of restricted effective population sizes can lead rapidly to extensive inbreeding of commercial broodstocks and declines in growth and reproductive performance.

A MICROCOMPUTER BASED SHELL ACTIVITY MONITOR FOR OYSTER DEPURATION SYSTEMS

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A sensitive microcomputer based shell activity monitor has been developed to measure valve movements of oysters in depuration systems. The monitor consists of a Zenith-100 microcomputer, a 12-volt lantern battery, a voltage control box, a linear variable displacement transducer (LVDT), an analog-to-digital converter, and appropriate software. The background variability of the system is small (±0.08 mm) compared to the maximum shell gape measured (7.51 mm).

The prototype developed uses only one LVDT; however the analog-to-digital converter is capable of accepting (virtually simultaneous) signals from 16 LVDT's. Thus, with only minor adaptations the system could be used to monitor the shell activity of up to 16 oysters at a time. Depuration systems can be monitored and optimized by information on the percentage of time that oysters are open. The monitor also has applications to related physiological studies of oyster pumping, feeding and respiration.

DISTRIBUTION, ABUNDANCE AND POPULATION STRUCTURE OF *CRASSOSTREA VIRGINICA* IN CARAQUET BAY, N.B. CANADA

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The most northerly commercially exploited population of American oysters, *Crassostrea virginica*, on the east coast of North America is located in Caraquet Bay, N.B. (latitude 47°50′). A quantitative assessment of the distribution, abundance and population structure of the public fishing area was conducted in June, 1987. A standardization of the transect sampling protocol (17 transects, each averaging 15 lm^2 samples) with previous studies (Lavoie 1977, Lavoie and Robert 1981) permitted a comparison with data collected in 1974 and 1979.

The distribution of the total oyster population indicated that the general area of the bed has changed slightly from 1974 to 1987. The oysters exhibited a typical heterogeneous distribution over the bed which accounts for the large variability in the data. The total population of the main bed showed changes in the distribution of high (>100 ind/m^2), medium (10-100/m^2) and low (<10/m^2) density beds from 1974 to 1987. The high density river channel beds have retained their integrity over time. In 1987, the average standing stock as total number and market size (length > 75mm) oysters for the main bed was 28.5 and 3.4 ind/m^2 respectively. This was lower than that observed in 1979 (43.7 and 6.7 ind/m^2, respectively) and 1974 (36.2 and 5.9 ind/m^2, respectively). Analysis of the size frequency data collected in 1987 showed that the population structure for each of the identified beds was distinct and that recruitment varied among beds. Comparison of the overall population structure among years indicated recruitment to the population is variable.

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COVER PHOTO: The American oyster, *Crassostrea virginica* (Gmelin) by J. Rollins

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COASTAL RESOURCE MANAGEMENT AND SHELLFISHING: A GLOBAL PERSPECTIVE

Selected papers from an international conference
held at

Hofstra University
Hempstead, New York

August, 1987

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INTRODUCTION

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In August of 1987 an international conference, "Coastal Resource Management and Shellfishing: A Global Perspective," was held at Hofstra University on Long Island, New York. The conference brought together a group of scholars, fisheries managers, and industry representatives to present papers and discuss the characteristics and problems of a variety of shellfisheries. While most of the cases presented were within the United States, papers were read treating fisheries in Scotland, Ireland, Mexico, Canada, The Netherlands, and Australia. The conference initiated a process which this special issue of The Journal is meant to continue: the development of a truly interdisciplinary approach both to understanding the problems of shellfishing resource management and to finding their possible solutions.

Managing coastal resources is a complex undertaking beset by minor and major crises. As these papers attest, it is just such difficulties which typically generate research. When the problem seems specific, such as pollution or pathogens, there is an obvious need for an accurate assessment of the nature and source of the substances in question. Hence the value of the procedures discussed by Blogoslawski et. al. and Robinson and Horzepa. Assessment of a wider range of variables is also necessary to respond to the more general environmental transformations wrought by natural or man-made restructuring of the environment. In this regard, the papers by Perret and Chatry on the ever changing coastal context of the Louisiana oyster fishery, Berrigan's on management's response to the hurricane devastation of the Florida oyster industry, and Dijkema on the Dutch response to constant flooding in the Zeeland estuaries of The Netherlands, all indicate the need for a detailed and accurate model of the ecosystem in order to either adjust to new conditions or change them. These papers also provide valuable methods for the building of such models.

Sometimes the problem manifests itself simply as a sudden or steady decline in landings, in which case research must be directed at a range of likely causes, from biological processes to overfishing. However, as anyone who has bothered to take a longer view of such industries will know, major challenges to the existence of shellfisheries arise at discouragingly regular intervals. Hargis and Haven recount the saga of the Chesapeake industry and van Ginkel presents an historical view of the Dutch shellfishing industry with which Dijkema's flood control project has been concerned. Such longitudinal case studies serve to remind us of the precarious adaptation of shellfish to fragile environments, and the consequent insecurity of industries dependent on them.

The key to survival under such circumstances, according to general Darwinian principles, is adaptability. In that game humans have the dual advantage of non-random mutations which are responsive to the environment and the Lamarckian inheritance of acquired characteristics. In other words, they can seek to understand the surrounding world, adjust their behavior accordingly, learn from their experience, and pass the learning on to others. But, as Hargis and Haven's paper reminds us, various groups of human beings are involved in this adaptive response, and each group's behavior may have economic, political, social, and cultural aspects which are as important to the nature of their response as they are ill-understood. Like the rest of us, fishermen are both part of the problem and part of the solution, but the dominant view of the human role in the ecosystem tends to be rather limited. They are seen as predators (especially when they take shellfish from natural beds) and sometimes as competitive users of the same environment (shippers, pleasure boaters, polluters). Efforts to understand the behavior of this species or of its sub-groups have been minimal and based on just the sort of "common sense" assessments and stereotypes that managers would find totally unacceptable for other species. Or else reliance has been placed on economic models which have proved of somewhat limited value in predicting the responses of fishermen.

Natural scientists may choose to ignore such problems, but the results of scientific research are implemented in a social context which determines their final form. Furthermore, as both Kassner and Siddall point out, managers as well as fisheries biologists too often find themselves surprised by the vehement opposition of fishermen to their proposed solutions, whether it be limited entry or the encouragement of aquaculture. It is not helpful to simply call fishermen too rational (in the economic self-interested sense) for opposing the former and irrational for not recognizing the benefits of the latter. Communities of fishermen have shared views of their significant social and natural environment. Their fishing behavior is based on their perception of how the natural world works, and their political behavior is based on their view of the motives of competitors, managers, government officials, and scientists. In both cases these models are based on real experience. If biolo-

gists feel that fishermen are naive and unscientific in their view of their natural environment, an experienced bayman may have a sounder understanding—and a wider accumulated data base—than most biologists do of the general socio-economic path of their industry. For example, if fishermen oppose any privatization of the commons, as Siddall discovered, it may be that their view of the eventual failure of any restrictions is more historically realistic. After all, many highly capitalized pursuits began as "cottage industries."

The papers by anthropologists included in this volume suggest another approach to the human role in shellfishing —both as users of the environment and actors in the problem solving process. The anthropological perspective focuses on humans not as isolated individuals but as members of groups, and from this point of view the social and cultural variation among relevant human populations is critical. The comparative perspective of this volume shows that if important differences in that respect exist among American shellfishermen, then an even greater variation can be found by looking elsewhere in the world. Such differences are not "natural," but rather cultural; other conditions have produced other fisheries. As the papers of Breton and Lopez Estrada, Dijkema, and van Ginkel show, the distribution of political power, relations to markets, and socio-cultural traditions of identity, co-operation, and competition all contribute to the local forms such fisheries take. The very perception of problems as such, as well as the problem-solving process, are also demonstrably affected by these factors, as is especially apparent in McCay's ethnography of the problem solving process in New Jersey's hard clam industry.

Some of the general differences between the United States and other countries in regard to the distribution of political power and property rights are particularly instructive. In Europe generally, centuries of communal rights of access to common property were combined with the "private," though entailed, rights of lords to both property and local political power. In varying degrees, the political development of nation-states was achieved through centralization, eventually leaving little power or authority at the local level. At the same time, commonages in land and water were privatized by an increasingly capitalist (rather than patrimonial) landlord class. For shellfishing this meant that the resources necessary to the pursuit, though they began as either the domain of local lords (secular or religious) or local "commons," became crown lands in the process of state formation, while land (and by extension, underwater land) in general was becoming increasingly viewed as an unrestricted commodity. Ironically, however, it is in precisely such regions that the great historical depth of shellfishing and other maritime pursuits meant deeply rooted customary tenure, the "communal property" of which van Ginkel speaks in his study of Yerseke in The Netherlands. Thus we have the potential for a great disparity between what is legal and what is locally legitimate. That was the political context of the innovations in the second half of the nineteenth century, when the development of oyster farming techniques required security of underwater tenure. As van Ginkel points out, the perceived "rational" economic interests of the Dutch state ensured that the forces of capital would prevail over local interests; the estuarine oyster grounds were auctioned to the highest bidders there in 1870. No matter how well defined, customary communalism made no headway against state-abetted class interests.

But the sovereign power of the State can have other effects on local circumstances. In Ireland and Mexico, for example, there have been national commitments to both the economic development and cultural preservation (often conflicting goals) of peripheral areas which—not coincidentally—are home to distinctive and threatened "ways of life" of ideological importance to the nation as a whole. This has generally meant support for local communities and communalism, which in this context take on romantic appeal. In Mexico there are the various Indian communities, and in Ireland the Gaelic speaking and insular West. Such national concern for these local worlds is often out of all proportion to their economic value, but ideology may or may not be accompanied by meaningful fiscal commitment. In any case, such attention to local community rarely means local political power. Decision making on resource management often still goes on in the capitals, where local realities cannot disturb firmly held stereotypes. As a result, local players jockey for access to middlemen who have access to such governing bodies.

Even within the confines of the United States, regional differences in property rights and political power have had a profound effect on the development of shellfisheries. While in most cases, the "common property" of the fisheries (e.g., natural oyster beds) have been both owned and managed by the states, there are regions where other legal and political traditions have made for interesting differences. A good case in point is Long Island, New York, discussed in this volume by both Kassner and Siddall. The erstwhile oyster rich lands beneath the Great South Bay, now the scene of a major hard clam industry, are under the control of local townships. This amounts to a survival from Puritan colonial days of the strong communal rights on which those settlements were based. Unlike European communal rights discussed above, however, these were based on free contractual association and have thereby survived through the political and economic development of the United States. However, there is also on Long Island the remnant of a very different tenure. Crown patents were granted to some aristocratic colonists, one of which included large underwater holdings passed on for generations through the Smith family and eventually purchased as private property by Blue Points Oyster Company. When secure tenure to town owned oyster grounds became an issue

in the second half of the nineteenth century, it was the township that came up with a plan for leasing underwater acreage. Efforts to democratize leasing failed, but not to the extent they did in Holland. On Long Island, privatization led to the development of a local elite, the planters and shippers of the famous Blue Points oyster industry (see Taylor 1983), but not the immediate and total capture of a local industry by outside entrepreneurs as in The Netherlands. In addition, township control gave local baymen access to management with the result that sizable sections of the bay remained town commons. Even where ownership and management are vested in the state, artisanal shellfishermen may have enough numbers to seriously affect state policy. This seems to be the case in Maryland, where the Chesapeake fishery has been to some extent protected from the forces of capital (and opened to the tragedy of the commons), in contrast to Virginia.

What does all this mean for the problems of managing coastal resources and shellfisheries? Jeffrey Kassner reminds us to consider "the consequence of baymen," and Siddall illustrates their role in the fate of aquaculture on Long Island. As Bonnie McCay's instructive contribution shows, the shellfishermen need to be understood not only as part of the problem but as part of the solution. Like all tribes, the fishermen, scientists, and government officials hold certain stereotypical notions of one another, and it is in the light of such views that behavior of these familiar strangers is interpreted. In these cases, as in all social interaction, the structure of the relationship has more bearing on understanding and behavior than the "objective" content of specific actions or communications. Thus, efforts must be made to alter those structures if a more productive interaction is to be achieved. McCay's paper, as well as many of the others here, indicates the need for a more holistic, ethnographic view of fishermen and other user groups, and for a management process that involves all relevant parties in every stage of the problem solving process. The former strategy would result in far better predictions of the reactions of these groups to natural and legal events, and the latter would do much to ensure fairness in management policy as well as a higher level of commitment and compliance.

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ENTRAINMENT OF DUNGENESS CRABS, *CANCER MAGISTER* DANA, BY HOPPER DREDGE IN GRAYS HARBOR, WASHINGTON

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ABSTRACT Grays Harbor, Washington, is a major center for the Dungeness crab fishery in Washington state, and potential impacts to the crab resource are a primary concern in the proposed widening and deepening of the existing Grays Harbor Navigation Channel. The Seattle District, U.S. Army Corps of Engineers, conducted crab entrainment studies in Grays Harbor to assess the effectiveness of a modified draghead in reducing crab entrainment and to gather entrainment data for use in impact analyses. Trawl samples were taken simultaneously with entrainment samples to compare entrainment rate with crab density in the navigation channel. Data analyses showed that the modified draghead was not effective in reducing crab entrainment. Entrainment rates varied greatly among different stations in the channel, and comparisons with trawl data showed that, on an area-swept or density basis (i.e., crabs per hectare), the dredge entrained an average of 26% of the crabs present in the area of the channel being dredged. There was a general linear relationship between entrainment rates and crab densities, and these data have been used to predict impacts on Dungeness crabs during project construction and to develop appropriate mitigation plans.

KEY WORDS: Entrainment, crab, *Cancer magister*, dredging

INTRODUCTION

Grays Harbor is a pear-shaped estuary located on the Washington coast, about 45 miles north of the mouth of the Columbia River and 110 miles south of the Strait of Juan de Fuca (Figure 1). The estuary is approximately 15 miles long and 11 miles wide, with a water surface area ranging from 91 square miles at mean higher high water (MHHW) to 38 square miles at mean lower low water (MLLW). Both the Hoquiam and Chehalis Rivers drain into the estuary and it is characterized by expansive mudflats and a series of intervening channels formed by the many rivers and creeks which empty into it (U.S. Army Corps of Engineers 1982).

Since the late 1800s, Grays Harbor has been a major west coast port for transportation of wood products to foreign nations. The growth of the log shipping industry and the increasing size of vessels have necessitated many improvements to navigation in Grays Harbor since the early 1900s. The U.S. Army Corps of Engineers (COE) maintains the navigation channel, which is currently 350 ft wide by 30 ft deep from the entrance to Aberdeen (Figure 2), and removes an average of 1.6 million cubic yards (cy) of dredged material annually. Most of the dredging is accomplished with pipeline and hopper dredges. At present, many deep draft vessels have difficulty entering and leaving Grays Harbor. The proposed project would widen and deepen the navigation channel to accomodate larger ships.

Grays Harbor is also an important commerical and sports fisheries area. Economically important shellfish species harvested here include Dungeness crabs (*Cancer magister* Dana), Pacific oysters (*Crassostrea gigas* (Thunberg)), and clams (native littleneck, *Protothaca staminea* (Conrad); butter clam, *Saxidomus giganteus* Deshayes; and razor clam, (*Siliqua patula* (Dixon)). The estuary is a major nursery habitat, particularly for Dungeness crabs, and contributes substantially to the coastal crab population (Armstrong and Gunderson 1985, Armstrong et al. 1984, Stevens and Armstrong 1984 and 1985). Although coastal crab landings for 1987–1988 are estimated at 15 million pounds, those over the last 10 years have averaged only 5.4 million pounds per year, with an annual value of approximately $4.6 million (Steve Barry, Washington Department of Fisheries, Montesano, WA., personal communication). Most of the crabs are landed at the city of Westport in Grays Harbor, the major center for the Dungeness crab industry on the Washington coast. The navigation project would benefit the commercial shipping and wood product sectors of the economy in the Grays Harbor area. However dredging activities related to the project would also affect the Dungeness crab resource to some extent and, therefore, the crab fishing industry.

Related Studies

In the last 20 years, there has been increasing public and agency concern regarding the impacts of dredging and dis-

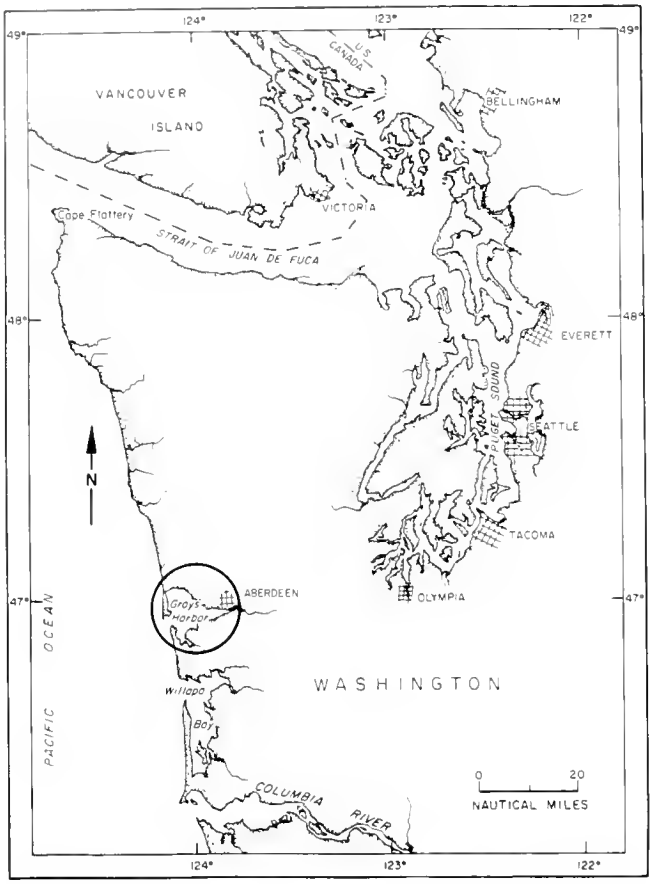

Figure 1. Map of Washington State showing the location of Grays Harbor.

posal on aquatic resources. Most early studies regarding dredging emphasized water quality and sediment contamination (Engler 1980), but more recent ones have focused on biological impacts, such as changes in species composition and diversity due to dredging (McCauley et al. 1977; Swartz et al. 1980; Poiner and Kennedy 1984; Taylor and Salomon 1968). LaSalle (1987) reviewed and summarized studies on the effects of dredging and disposal to provide guidance to the COE on seasonal restrictions for dredging and disposal.

Of the studies conducted in the United States, few have assessed impacts of direct uptake, or entrainment, by dredges to mobile epibenthic organisms or demersal fish. Some of the first entrainment research on fish was conducted in Canada in the early 1970s when observations suggested mortality to salmon fry which were being discharged from a pipeline dredge operating in the lower Fraser River in British Columia (Braun 1974 a,b; Dutta and Sookachoff 1975 a,b). Quantification of entrainment and mortality rates eventually led to establishment of dredging guidelines for that area (Boyd 1975; Arsenault 1981).

Consideration of direct impacts from dredging to commercially important shellfish species has focused on oysters and crabs. The Baltimore District COE and Waterways Experiment Station of the COE co-sponsored a workshop in 1985 to discuss the significance of entrainment of larval oysters by hydraulic cutterhead dredges (American Malacological Union 1986). Predictions of mortality rates based on proposed entrainment models presented at the workshop ranged from 0.005 to 0.3% for late stage larvae (Carriker et al. 1986) and up to a maximum of 88% for all larval stages (Carter 1986). However, those are theoretical models and have not been tested in the field.

Actual entrainment studies of shellfish are limited to Dungeness crabs. Larson (1985) conducted several studies on the Columbia River bar aboard the Corps dredge ESSAYONS and found that over 99% of the crabs collected in eight cruises were smaller than 25 mm. Some work has also been done in Canada to assess the effects of pipeline dredges on Dungeness crab (Archibald 1983).

Most entrainment studies on the west coast that have dealt with Dungeness crabs have been conducted in Grays Harbor, Washington. In the mid 1970s Seattle District Corps of Engineers initiated a series of studies in Grays Harbor to determine the potential impacts of maintenance dredging on biological resources, including Dungeness crabs. The studies evolved out of meetings between the COE, representatives of state and federal agencies, and fishermen. Data collection included surveys of crab populations in Grays Harbor as well as crab entrainment studies on several types of dredges (U.S. Army Corps of Engineers 1980).

The first Dungeness crab entrainment study in Grays Harbor was conducted in 1976 by Tegelberg and Arthur (1977) on hopper and pipeline dredges. However, the results were inconclusive because of problems with the sampling gear and methodology. Stevens (1981) improved on the previous study by quantifying entrainment on the basis of cubic yards of material dredged. He also gave a detailed account of sampling methodology for entrainment studies done on hopper, pipeline, and clamshell dredges; derived estimates of total crab mortality for maintenance dredging; and estimated crab populations at several locations in Grays Harbor.

As plans developed for construction of a wider and deeper navigation channel in Grays Harbor, more information was needed to assess potential impacts to crabs from project construction as well as additional maintenance dredging which would be required after completion. Population studies in the estuary were intensified and expanded to nearshore areas (Armstrong and Gunderson 1985; Armstrong et al. 1984, 1985, 1986; Dumbauld et al. 1987). Armstrong et al. (1982) collected additional entrainment and mortality data, for crabs and other species, including sand shrimp (*Crangon sp.*) and fish. They also attempted to relate crab entrainment rates to etimated crab population densities from trawl samples, but the trawl samples were not synchronous with dredging samples and could not be used in a predictive model.

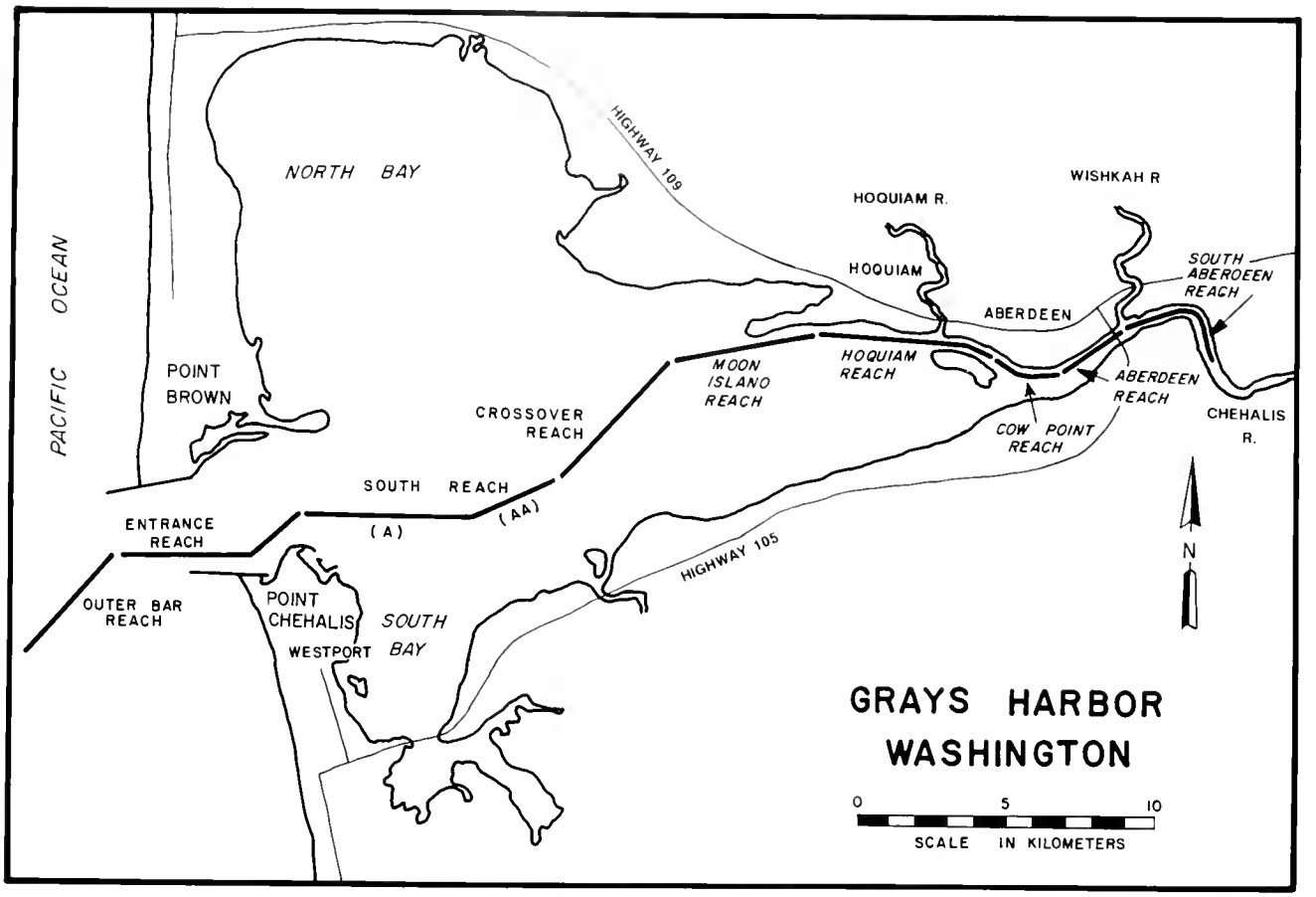

Figure 2. Map of Grays Harbor showing the location of the navigation channel.

Planning and Implementation

The concern regarding loss of crabs to the fishery resulted not only in data collection to predict impacts but development of approaches for avoiding or mitigating crab losses. In August and September 1984 the Seattle District COE convened a panel of experts consisting of agency representatives, engineers, commercial crabbers, and crab biologists to evaluate and recommend solutions for minimizing impacts to crabs. One of the recommendations of the panel was the modification and testing of a draghead (Pearson 1985). The idea was based on a similar concept used by the COE in Florida to avoid entrainment of sea turtles (Joyce 1981).

A modified draghead was designed and constructed by Portland District COE and tested in October 1985 and August 1986 aboard the Corps dredge YAQUINA. Improved sampling apparatus and methodology provided an opportunity to collect more accurate entrainment data than previous studies as well as to evaluate the performance of the modified draghead. In addition, concurrent trawl samples were conducted by University of Washington biologists, under contract to the COE, to provide baseline population data for comparison. The August 1987 sampling effort was solely for gathering more entrainment data.

The specific objectives of the study were: 1) to gather information for determining the impact of dredging on Dungeness crabs in Grays Harbor; 2) to test a piece of equipment designed to minimize entrainment and mortality of crabs by hopper dredge; and 3) to relate entrainment rates to *in situ* crab densities in the navigation channel.

SAMPLING LOCATIONS

Entrainment samples were taken in the South Reach of the Grays Harbor Navigation Channel in October 1985, August 1986, and August 1987 (Figure 3). The October 1985 sampling was conducted at Station 2 in the South Reach of the navigation channel to minimize interference with maintenance dredging operations and to sample in an area of the channel with high crab densities. Three additional stations (Stations 1, 3, and 4) were included for comparison during August 1986 and two more (Station 1.5 and the Bar Station) in August 1987 (Station 4 was eliminated from the 1987 schedule due to sampling difficulties at that location). The stations were approximately 914 m long, which corresponded to the distance usually required for filling one-half of the hopper, or about 410 c.y. of dredged material. Normally, the dredge will traverse 914 m (termed a "pass" or "cut"), turn, and dredge over the same area to

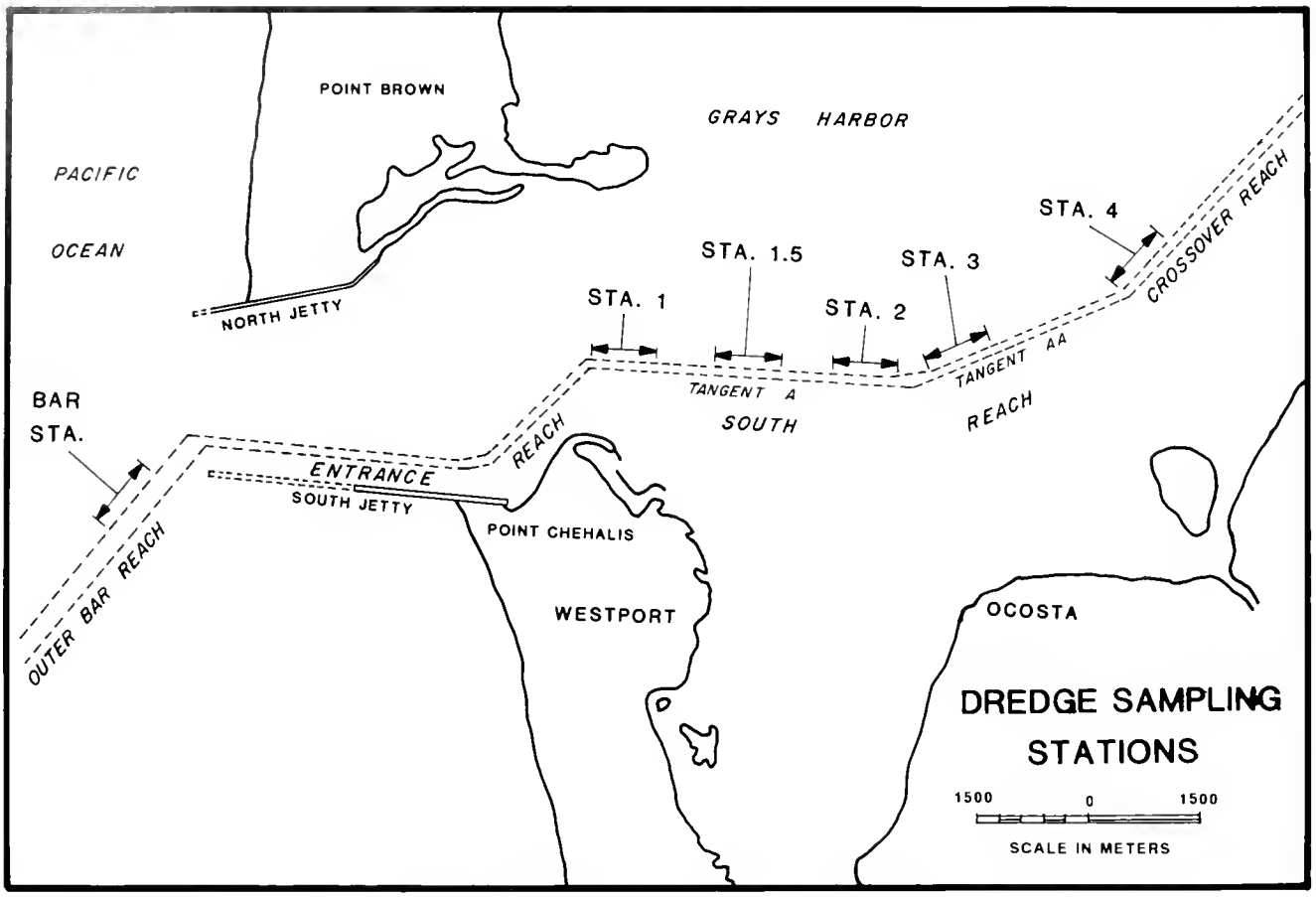

Figure 3. Map of Grays Harbor showing the location of sampling stations.

complete a load, then dispose of the material. The passes are repeated in a given area until the appropriate depth is attained before the dredge moves to another location.

SAMPLING METHODS

Two different sampling methods were employed during the study. The first, aboard the dredge, involved monitoring dredged material from each draghead by filtering it through collection baskets on deck. This was done in order to compare entrainment rates for the modified and the unmodified dragheads (in 1985 and 1986) and to obtain as much entrainment data as possible.

In the second sampling method, trawls were performed before, during, and after entrainment tests in order to estimate crab populations in the channel (Dinnel et al. 1986, 1987, and Dumbauld et al. 1988). Trawling was conducted with a 3-meter plumb staff beam trawl specifically designed to capture crabs (Gunderson et al. 1985). All crabs caught in trawl and dredge samples were counted, measured (carapace width anterior of the 10th anterolateral spine), and sexed. The sex of most crabs sought in dredge samples was determined; however some were either too small or were missing abdominal plates and gender could not be distinguished. Crab density was determined from trawl and dredge catches by calculating the area swept by either the trawl or the dragheads and expressed as the number of crabs per hectare (crab/ha). Crab entrainment figures were also calculated on a volumetric basis, or number of crabs entrained per cubic yard (crabs/cy) of material dredged.

A prototype modification of a slotted California-type draghead (Figure 4A) was designed and constructed by the Portland District Corps of Engineers. The modification consisted of a screen made out of 50 mm mesh galvanized cyclone fencing (72 mm diagonal) welded to the sides of the draghead (Figure 4B), which covered the side slots of the draghead but would not impede the operation of the draghead. One of the premises for the modification was that most crabs were entrained by being pulled through the side slots of the draghead and that the screen would substantially reduce entrainment.

The main objective of the modification was to decrease the entrainment of Dungeness crabs greater than one year old (1 + crabs) by the hopper dredge. In Grays Harbor, 1 + crabs are generally larger than 70 mm during summer months, and are considered to be an important resource, since they will enter the fishery within the next two or three years (Armstrong et al. 1987).

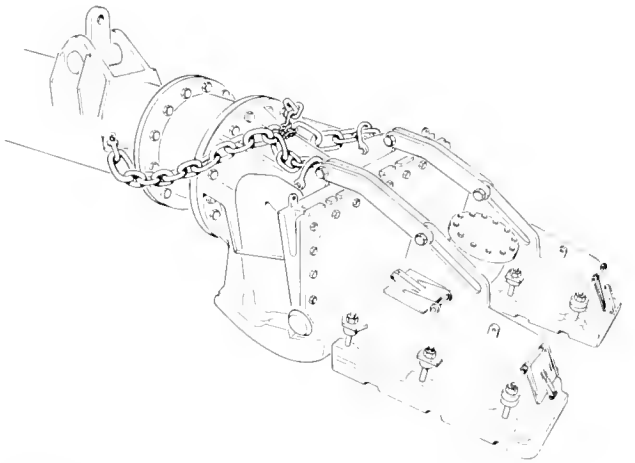

Figure 4A. Drawing of a California-type draghead used on the YAQUINA.

To test the modified draghead, a collection basket was also devised (Figure 5A) for sampling discrete amounts of dredged material. In this way crab entrainment could be accurately estimated in terms of volume of material dredged and also the area swept by each draghead. The collection baskets were installed on the starboard and port sides of the Corps dredge YAQUINA, along with a diversion system (Figure 5B).

During sample collection, all dredged material from each draghead was diverted to the collection baskets for a specified period of time. After initial sampling, we determined that 30 seconds was the optimal time period; using longer times clogged the samplers and damaged crabs. At least three replicate samples were taken for each "pass" of the dredge, or a minimum of six samples per hopper load.

Calculations

Catches of Dungeness crabs from trawl samples were calculated as number of crab per hectare by the following formula:

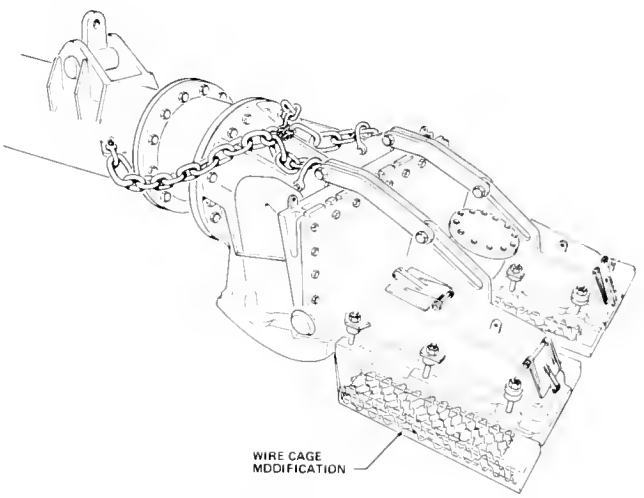

Figure 4B. Drawing of the modified draghead used in the entrainment study on the YAQUINA.

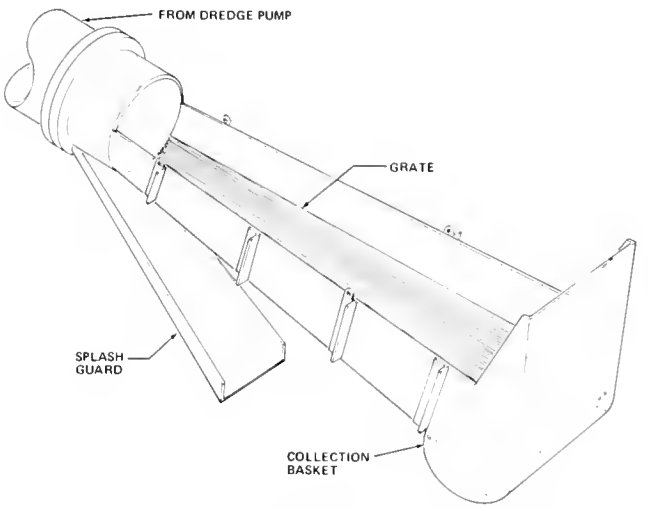

Figure 5A. Drawing of the crab collection basket used in the entrainment study on the YAQUINA.

$$\text{Catch} \times 10{,}000/\text{area swept} = \text{no. of crabs/hectare}$$

where area swept = trawl distance in meters (m) × width of the net opening (2.3 m).

Distance covered by the trawl was determined by radar ranges on navigation aids. Each tow was approximately 10 minutes in duration and swept an area of approximately 1,065 m^2. At least ten replicate beam trawls were taken at each station, and results were averaged for each station and

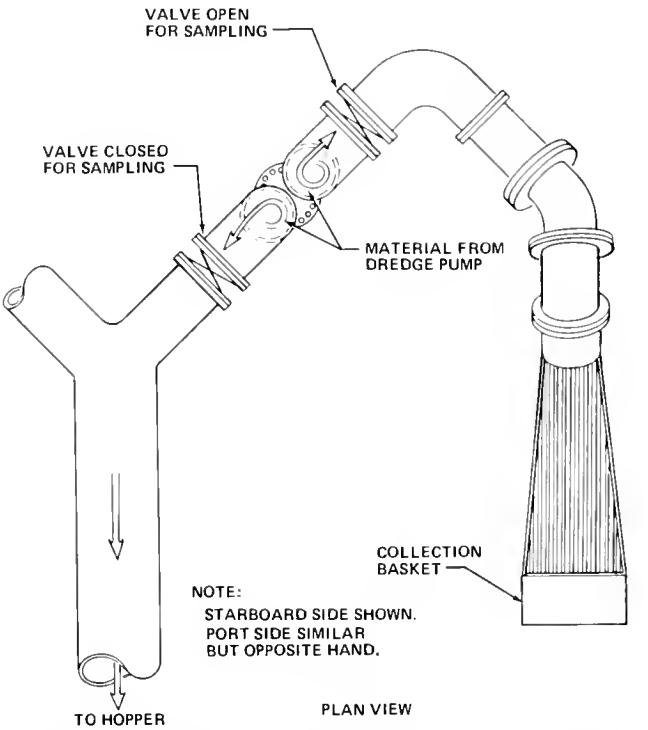

Figure 5B. Schematic drawing of the distribution system for the crab collection baskets aboard the YAQUINA.

according to time sequence (i.e., before, during, or after dredging) (Dinnel et al. 1986, 1987; Dumbauld et al. 1988).

The area swept by the dragheads of the hopper dredge was calculated similarly. For the dragheads that were used on the YAQUINA, modeling studies have shown that the effective dredging width of the draghead when stationary is 1.5 × width (i.e., 1.2 meters) of the draghead = 1.8 meters (m). The area swept can then be obtained by the following:

$$A = 1.8\ m \times D$$

where A = the area (in m^2) covered during sampling (for one draghead); 1.8 m is the effective dredging width of the draghead, and D = distance (m) traversed by the dredge during a sample.

Entrainment rates were also calculated on a volumetric basis as the number of crabs per thousand cubic yards of material dredged (crab/kcy). The volume of dredged material during sampling was obtained from instruments on the bridge of the YAQUINA. Readings of loading rates were taken at the time of sampling for improved accuracy, since rates can vary according to the speed of the dredge and the type of substrate. Loading rates during sampling averaged about 10–15 cubic yards/minute, well within the normal operating range of the YAQUINA.

RESULTS AND DISCUSSION

The total numbers of crabs caught in samples aboard the dredge are summarized by date and location in Table 1. Totals and catch by each draghead are also shown; the dragheads are designated as modified or unmodified for the October 1985 and August 1986 data, when the modified draghead was tested.

Entrainment Rates

Entrainment data were analyzed for several purposes: to determine the effectiveness of the modified draghead in excluding larger crabs; to compare day and night catches; and to examine the relationship between dredge entrainment and crab density. The dredge data were not normally distributed, since crabs were absent from many of the replicates. This precluded the use of parametric tests such as analysis of variance or t-test to test for differences between the modified and unmodified dragheads. Therefore, we used nonparametric sign tests (the null hypothesis being that the entrainment rates are the same for both dragheads). In this test (Table 2), the two treatments (i.e., modified vs. unmodified draghead) were compared simultaneously by counting the number of times a greater number of crabs (indicated by a plus) or fewer number of crabs (indicated by a minus) were entrained by the modified draghead versus the unmodified draghead. Tied ranks (indicated by a zero) were noted but were not used in the analysis. In instances where an uneven number of samples resulted, usually due to clogging of a collection basket on one side, only simultaneous samples were considered.

Sign test analyses showed that the October 1985 samples had the widest differences, with 10 minuses and 3 pluses ($p = 0.09$). Data from the October 22–23, 1985 and August 1986 studies had even smaller differences, with p values ranging from 0.52 to 1.0. When all August stations were combined, there were a total of 36 minuses and 35 pluses, with 78 tied ranks and 151 null catches (total n = 300). The statistical evidence supported the null hypothesis that the entrainment rates for the modified and the unmodified draghead are the same. Data from both dragheads were then pooled for further analysis below.

Chi-square tests (Zar 1984) were used to test the hypothesis that entrainment rates were the same for day and night samples (Table 3). Only those data were included from stations which were sampled both day and night. Analyses showed no significant differences between the distribution of counts for day samples vs. night samples.

Pooled data from both dragheads were used to compare entrainment rates on a density and volumetric basis. Entrainment varied widely from one sampling period to another and also from one station to another (Table 1). The lowest entrainment rate (46 crabs/kcy or 48 crabs/ha) occurred in South Reach during the October 18, 1985 sampling. However, this rate tripled several days later to 118 crabs/kcy, indicating the degree of fluctuation in crab populations. The highest entrainment rate observed during August 1986 was 500 crabs/kcy (519 crabs/ha) at Station 2, and decreased with distance up the channel to 79 crabs/kcy at Station 3 and 58 crabs/kcy at Station 4. Entrainment rates in August 1987 varied from 133 crabs/kcy (172 crabs/ha) at Station 2 up to 9,367 crabs/kcy (11,222 crabs/ha) at the Bar Station. The extremely high entrainment rate at the latter station was due to the very dense population of newly settled young-of-the-year (YOY) crabs in that area, a different situation from the other stations where mostly one year old crabs were caught.

Since dredge production is reported in cubic yards of material dredged, the volumetric entrainment rate (crabs/kcy) is perhaps the more useful measurement. Entrainment rates for this study and previous entrainment studies in Grays Harbor are presented in Table 4. There is a wide variation in rates, not only from one location to another, but from one season to another. For example, rates in South Reach are both the highest (500 crab/kcy in August, 1986) and the lowest (46 crab/kcy in October, 1985). In general, the highest entrainment rates were observed in South Reach. This is a function of the distribution of the crab population in Grays Harbor, with the majority of crabs inhabiting outer portions of the harbor, and decreasing in numbers upstream (Armstrong et al. 1987). In addition, studies strongly indicate that 1+ crabs tend to migrate into the estuary during late spring and out of the estuary during late summer to early fall; this could account for high den-

TABLE 1.

Summary of entrainment data for 1985, 1986, and 1987. Entrainment rates are given in terms of volume of material dredged (crabs/kcy) and density (crabs/ha).

		NUMBER OF CRABS				ENTRAINMENT RATES	
Date	Location	Modified Draghead	Unmodified Draghead	Total no. of crabs	Total no. of samples	No. crabs/kcy	No. crabs/ha
Oct 18, 1985	Station 2, South Reach	11 (n = 22)	19 (n = 21)	33	43	46	48
Oct 22–23, 1985	Station 2, South Reach	20 (n = 64)	24 (n = 64)	44	128	118	145
Aug 1–4 1986	Station 1, South Reach Tangent A	23 (n = 60)	35 (n = 61)	58	121	155	192
	Station 2, South Reach Tangent A	76 (n = 48)	64 (n = 48)	140	96	500	519
	Station 3, South Reach Tangent AA	2 (n = 15)	7 (n = 16)	9	31	79	127
	Station 4, Crossover Reach	6 (n = 26)	3 (n = 26)	9	52	58	58
		Port Draghead	Starboard Draghead				
Aug 1–3 1987	Station 1, South Reach Tangent A	47 (n = 48)	25 (n = 47)	72	95	222	266
	Station 1.5, South Reach Tangent A	61 (n = 47)	51 (n = 47)	112	94	397	419
	Station 2, South Reach Tangent A	31 (n = 48)	14 (n = 44)	45	92	133	172
	Station 3, South Reach Tangent AA	48 (n = 48)	34 (n = 46)	82	94	224	307
	Bar Station Bar Reach	1001 (n = 42)	1679 (n = 42)	2680	84	9,367	11,222

sities of crabs in the entrance and south reaches of the channel during those times, hence higher entrainment rates (Armstrong et al. 1985, 1986, 1987; Dumbauld et al. 1987).

Entrainment rates from previous studies can be used in conjunction with dredge production for gross estimates of crab impacts. However, such estimates rely on a constant entrainment rate and make no allowances for changes due to crab population densities in various reaches or seasons. One of the objectives of the present study was to determine what relationship existed between entrainment rates and crab density. A priori, it was clear that such a relationship should have two characteristics: 1) the number of crabs entrained should generally increase as crab density increases, and 2) entrainment should be zero when density is zero. With enough data, it may then be possible to predict entrainment from dredging on the basis of trawl samples, eliminating the need for very costly dredge samples.

In fitting statistical models to data, the best approach is to start with a simple (e.g., linear) model and assess its adequacy of fit. Regression analysis of paired trawl and entrainment data from October 1985 and August 1986 (Table 5) showed a highly significant correlation between those two variables ($r^2 = 0.98$). Another study was conducted in 1987 to augment existing data and to verify the density dependent concept of entrainment. The Bar Station was added because a large proportion of project dredging would occur there. However, trawling at the bar station was difficult because of sea conditions and uneven bottom contours, resulting in gear inefficiency. Discrepancies both in numbers and sizes of crabs caught by the dredge and trawl precluded use of trawl data from the Bar Station in the regression analysis.

With the addition of 1987 data (Table 5 and Figure 6), a general linear relationship was still evident between entrainment and crab density, although the amount of vari-

TABLE 2.

Results of sign tests comparing crab entrainment rates for the modified draghead vs. the unmodified draghead, by station and date.

Date	Location	Number of +s	Number of −s	Number of 0s*	Number of null samples	Total no. of samples	p value**
Oct 18, 1985	Station 2, South Reach	3	10	8	22	43	0.09
Oct 22–23 1985	Station 2, South Reach	9	13	42	64	128	0.52
Aug 1–4 1986	Station 1, South Reach	12	15	33	61	121	0.70
	Station 2, South Reach	19	16	13	48	96	0.74
	Station 3, South Reach	1	3	11	16	31	0.63
	Station 4, Crossover Reach	3	2	21	26	52	1.00
All August	Stations	35	36	78	151	300	1.00

* Zeros (0s) refer to tied ranks, or simultaneous samples in which the same number of crabs were caught by each draghead. Tied ranks were not used in data analysis but are included for comparison.

** The p value is based on comparison of the number of +s and −s.

ability among the nine data points was clearly greater than that with the 1985 and 1986 data, resulting in a lower, albeit significant, coefficient of determination ($r^2 = 0.25$, $p = 0.08$, one sided). The intercept (20 crabs/kcy), however, was not significantly different from zero, and there was no evidence for significant lack of fit ($p > 0.10$). Two data points, (1561, 133) and (1413, 500), had large residuals of similar values, but in opposite directions, and were identified using Cooke's Distance Measure (Weisberg 1985) as being very influential in determining the fitted line. Upon recomputation without the two influential points, we found that the coefficient of determination increased ($r^2 = 0.40$), but that the intercept (i.e., −112) was significantly different from zero, necessitating the procedure of forcing the line through the origin to maintain a biological meaning. When this was done, the slope was 0.24 very close to the previous value of 0.21 obtained with the nine-point regression analysis. The fact that the slope remained essentially the same when the two influential data points were removed, and that an ordinary, unrestricted fitted line for the nine data points gives an intercept not significantly different from zero as well as an r^2 value which is significant at the 0.08 level (one-sided), lends credence to using the line to help predict crab impacts.

TABLE 3.

Chi-square results for day vs. night entrainment rates stations at which day and night samples were taken.

Date/Station		Crab Count 0	1	>2	Chi-square value	P value*
October 1985						
Station 2	Day	22	12	9	1.38	.50
	Night	24	14	5	(Not significant)	
August 1986						
Station 1	Day	26	12	10	.62	.73
	Night	5	4	3	(Not significant)	
Station 2	Day	8	9	15	3.9	.14
	Night	1	4	13	(Not significant)	
August 1987						
Station 1	Day	4	3	9	.96	.62
	Night	9	9	13	(Not significant)	
Station 1.5	Day	9	7	19	.40	.82
	Night	2	3	6	(Not significant)	
Station 2	Day	13	7	4	.48	.79
	Night	10	5	5	(Not significant)	
Station 3	Day	5	10	3	2.07	.35
	Night	9	10	9	(Not significant)	

* Degrees of freedom = 2

Comparisons of entrainment rates on an area-swept or density basis (crabs/ha), with corresponding trawl densities (Table 5) provided an estimate of the percent of the crab population in the dredged area that was entrained and showed that the dredge entrained, on the average, less than 27% of the crabs present. Except for the bar station, trawl density estimates were assumed to be 100% of the crab population in the channel for purposes of comparison with entrainment data (Dinnel et al. 1986, 1987; and Dumbauld et al. 1988). The trawl was relatively inefficient at the Bar Station and data for the trawl and dredge are not comparable. For the stations inside the harbor, results indicate that crab entrainment rates (i.e., crab/ha) generally increase with density, with the highest proportional entrainment rate (53%) occurring at Station 1 in August 1987.

One factor which may have contributed to the disparity in crab catches between the trawl and dredge was dredge speed. Although both the dredge and trawler operated at approximately one knot when sampling, the dredge speed

TABLE 4.

Comparison of hopper dredge entrainment rates from studies in Grays Harbor, Washington.

Source	Dredge	Date of Study	Location	Entrainment Rate (crabs/kcy)
Tegelberg and Arthur, 1977	PACIFIC	March 1975	Crossover and South Reaches	131–327
Stevens, 1981	SANDSUCKER (hopper-barge)	Nov–Dec 1978	South Reach	233
	PACIFIC	March 1979	South Reach	182
Armstrong et al. 1982	SANDSUCKER	June 1980	Cow Point Reach	79
		July 1980	South Reach	502
		August 1980	Moon Island Reach	107
		May–Sept 1980	Crossover Reach	75
Present Study	YAQUINA	Oct 18 1985	Sta 2 South Reach	46
		Oct 22–23 1985	Sta 2 South Reach	120
		Aug 1–4 1986	Sta 1 South Reach (Tangent "A")	155
			Sta 2 South Reach (Tangent "A")	500
			Sta 3 South Reach (Tangent "AA")	79
			Sta 4 Crossover Reach	58
	YAQUINA	Aug 1–3 1987	Sta 1 South Reach (Tangent "A")	222
			Sta 1.5 South Reach (Tangent "A")	397
			Sta 2 South Reach (Tangent "A")	133
			Sta 3 South Reach (Tangent "AA")	224
			Bar Station Bar Reach	9,367

decreased occasionally in order to maintain maximum loading rates. This would have provided the crabs more opportunity to avoid the draghead. Another possible explanation is that the front of the draghead tends to bury in the substrate as it moves forward, acting as a plow and displacing some material to the side and, therefore, any crabs contained within it.

The entrainment data have important implications for project construction. The relationship between trawl density and entrainment rates (Figure 6) forms the basis of a computer model to predict impacts to crabs (Armstrong et al. 1987) and the dredging schedule has been planned, using model predictions, to avoid impacts as much as possible. Thus, crab losses can be minimized, even though the draghead modification proved unsuccessful. In addition, the impact predictions will be used to develop a crab mitigation plan consisting of the creation of oyster shell habitat for juvenile crabs.

Crab Size and Sex Composition

For the 1985 and 1986 samples, mean crab sizes were compared for each draghead to determine if any significant differences existed, indicating size selectivity with the modified draghead. Size and sex ratio data were also compared to trawl data to see if the dredge entrained crabs in a similar, although proportionately lower, manner. It should be noted that not all crabs caught in dredge samplers were measurable; therefore, the number of measured crabs does not correspond to the total number entrained. Also, sex could not be determined for all crabs that were measurable, either due to immaturity or absence of abdominal plates.

Measurable crabs entrained aboard the dredge during the October 1985 and August 1986 studies had overall average sizes of 85mm and 101mm, respectively (Figure 7). There were no significant differences in the mean sizes of crabs entrained by the modified draghead and the regular draghead or between the mean sizes of male and female crabs, either at individual stations or for all stations combined ($p > 0.25$ for all size data comparisons). These data, in conjunction with entrainment rates for the modified and unmodified dragheads, confirmed that the draghead modification was not effective in reducing entrainment of larger crabs.

Comparisons of dredge and trawl data for 1985 and 1986 (Figure 7) showed that crab sizes were approximately the same, except for Station 4 in 1986 where dredged crabs averaged about 20mm larger. However, the dredge and

TABLE 5.

Comparison of estimated trawl crab densities in crabs per hectare (crabs/ha) and entrainment rates in crabs/ha and crabs per thousand cubic yards (crabs/kcy).

Date	Location	Crab density (Trawl)* Crabs/ha	Entrainment Rate Crabs/ha	Proportion of crabs entrained by dredge (Trawl = 100%)	Entrainment Rate Crabs/kcy
Oct 18 1985	Station 2, South Reach	506 (n = 22)	48 (n = 43)	10%	46 (n = 43)
Oct 22–23 1985	Station 2, South Reach	773 (n = 22)	145 (n = 128)	19%	118 (n = 128)
Aug 1–4 1986	Station 1, South Reach Tangent A	816 (n = 14)	192 (n = 121)	23%	155 (n = 121)
	Station 2, South Reach Tangent A	1,413 (n = 13)	519 (n = 56)	37%	500 (n = 56)
****	Station 3, South Reach Tangent AA	**	127 (n = 31)	**	79 (n = 31)
	Station 4, Crossover Reach	639 (n = 12)	58 (n = 52)	9%	58 (n = 52)
Aug 1–3 1987	Station 1, South Reach Tangent A	504 (n = 13)	266 (n = 95)	53%	222 (n = 95)
	Station 1.5 South Reach Tangent A	972 (n = 8)	419 (n = 94)	43%	397 (n = 94)
	Station 2, South Reach Tangent A	1561 (n = 8)	172 (n = 92)	11%	133 (n = 92)
	Station 3, South Reach Tangent AA	968 (n = 8)	307 (n = 94)	32%	224 (n = 94)
****	Bar Station Bar Reach	94*** (n = 20)	11,222 (n = 84)	***	9,367 (n = 84)

* Dinnel et al., 1986 and 1987 and Dumbauld et al., 1988

** Corresponding trawl data not available

*** Trawl not assumed to be 100% efficient on the bar due to sea conditions, bottom topography, and small size of crabs

**** Station not included in regression analysis

n = number of samples

trawl means at Station 4 were not significantly different and the mean size of all measurable crabs collected by the dredge was 101 mm, identical to that of the trawl samples. Of the crabs entrained by the dredge that could be sexed, the proportion of males was approximately 62% in October 1985 samples and 86% in the August 1986 samples. The corresponding compositions of trawl samples were 43% and 66% males, respectively. The higher percentage of male crabs is consistent with past work showing that mature females usually migrate out of the estuary by the beginning of their third year (Armstrong and Gunderson 1985; Armstrong et al. 1982, 1987; Dinnel et al. 1986). Despite the fewer numbers of crabs collected by the dredge, data on crab size and sex ratio indicated that the dredge was entraining crabs in approximately the same proportions for these parameters as trawl samples.

In August 1987 the proportion of male crabs was 75% in dredge samples and 80% in trawl samples. Average crab sizes for both dredge and trawl samples were noticeably smaller than those for the previous two years (Figure 8). Also, with the exception of Station 3, the mean carapace widths of entrained crabs at each station differed significantly from those caught in the trawl.

Differences were most pronounced at the Bar Station, where the dredged crabs averaged 11mm, compared to 67mm for trawl samples. As noted previously, several factors affected trawl efficiency at that station to produce the large discrepancy between the mean crab sizes for the dredge and trawl.

The grand averages for all inner harbor stations in 1987 showed that the crabs caught by the trawl were generally larger than those entrained by the dredge (67mm and

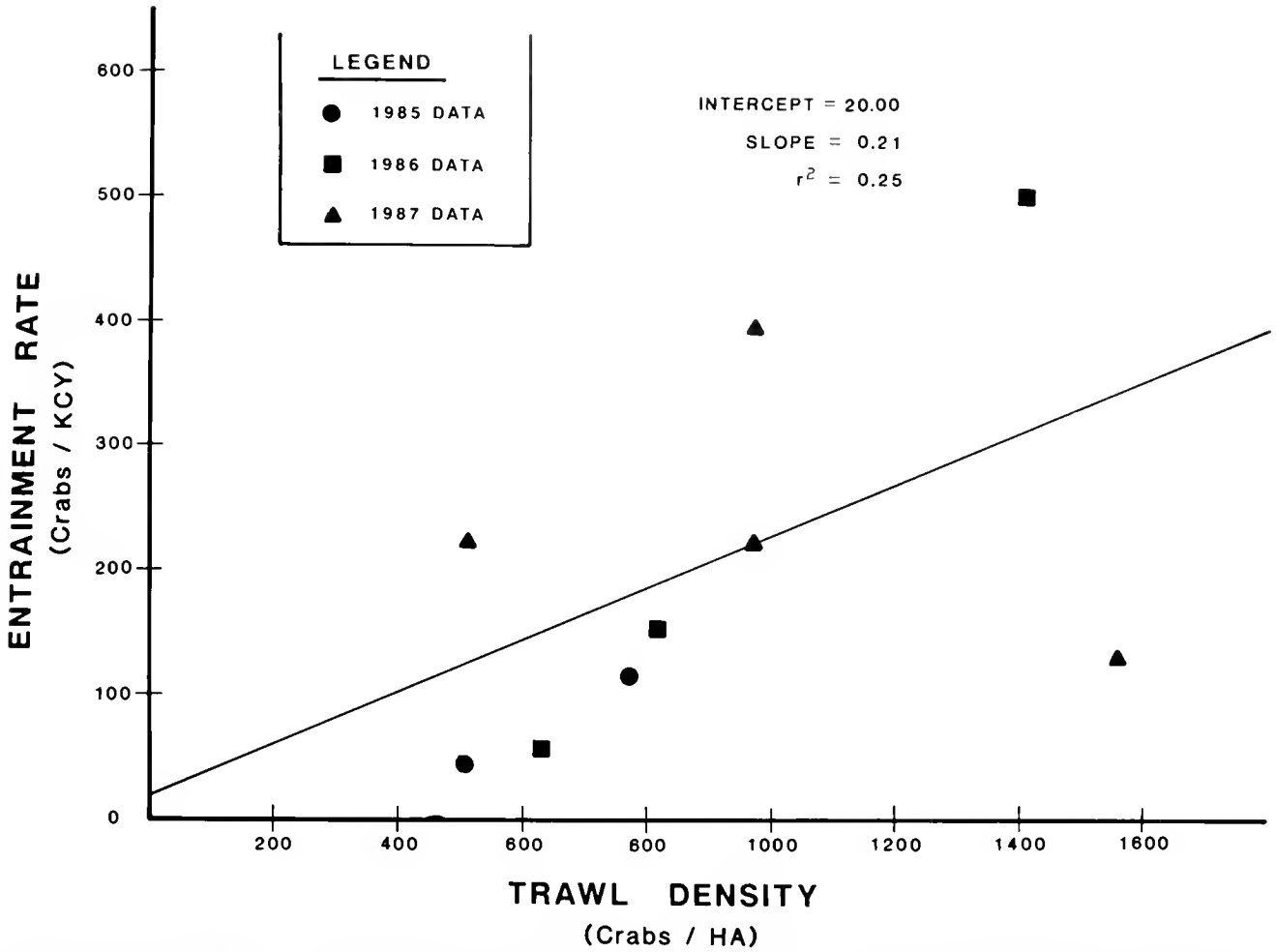

Figure 6. Linear regression of average crab entrainment rates (crabs/kcy) and densities from trawl samples (crab/ha) for 1985, 1986, and 1987. The points correspond to data in Table 5.

55mm, respectively). Some of these differences may be explained by the large proportion of young-of-the-year, 0+ crabs (i.e., less than 45mm in carapace width), which greatly skewed both averages (Dumbauld et al. 1988).

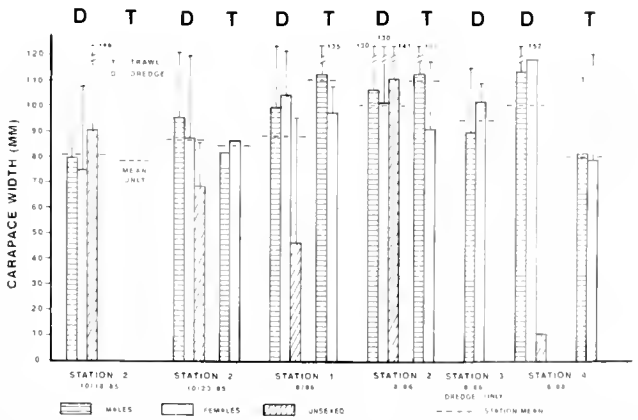

Figure 7. Average carapace widths (± sd) for crabs caught in dredge and trawl samples in 1985 and 1986, summarized by station and date.

Mortality

In attempting to relate crab entrainment to mortality, it is important to note that the two events are not necessarily synonymous. Mortality depends on many factors, including the type of dredge (e.g., hopper, pipeline, or clamshell), size of the crabs, disposal location (confined or open water), and speed of the dredge. Gross mortality estimates from the present study were made on the basis of crabs caught in the samplers which were obviously injured or mutilated. In the October 1985 samples, 24% of entrained crabs were mutilated or had obvious injuries which eventually would cause death. The average mortality rate for August 1986 samples were slightly lower, 16.6%.

Entrained crabs were scrutinized more closely for injuries during the August 1987 study. In addition to dead crabs, those which were missing appendages or had cracked carapaces were counted as mortalities. The highest mortality rate (50%) was recorded at Station 3, with an overall average at inner harbor stations of 41%. Mortality at the Bar Station was much lower, 20%, because of the smaller size of crabs in that area.

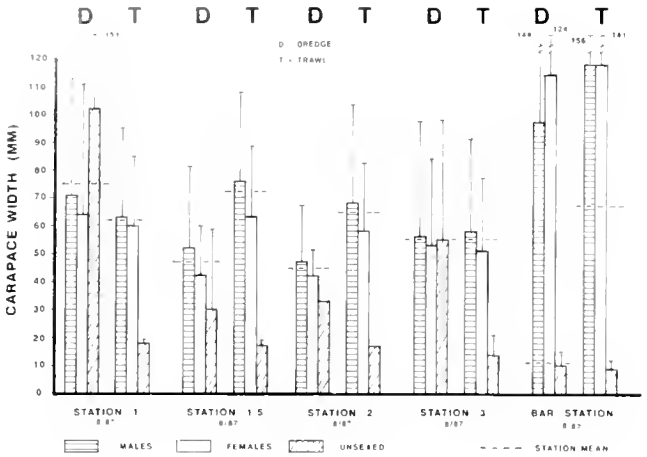

Figure 8. Average carapace widths (± sd) for crabs caught in dredge and trawl samples in 1987, summarized by station and date.

Estimates of dredge related mortality of larger crabs in the present study were relatively low compared to those of previous workers. Stevens' estimates ranged from less than 10% for all size crabs entrained by clamshell dredge up to approximately 75% for hopper dredges (Stevens 1981). Armstrong et al. (1982) estimated mortality rates as high as 86% for larger crabs (i.e., >50mm in carapace width) entrained by hopper dredges.

Other studies aboard the Corps dredge ESSAYONS on the Columbia River bar indicated that mortality rates for small crabs (1% to 5% for crabs less than 10 mm in carapace width) are much lower than expected (Kim Larson, Portland District Corps of Engineers, Portland Oregon, personal communication). The small crab pass through the pump virtually unharmed, whereas larger crabs may be crushed by the pump mechanism or harmed by debris such as wood and rocks that may also be sucked into the drag-arms. Related experiments have demonstrated that, regardless of size, uninjured crabs which enter the dredge hopper have very high survival rates, even after being exposed for two hours to pressure equivalent to that at the bottom of a full hopper load (Larson 1986).

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RECRUITMENT OVERFISHING IN A TROPICAL SCALLOP FISHERY?

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ABSTRACT The fishery for saucer scallops *Amusium japonicum balloti* is an important component of a multi-species trawl fishery for shellfish on Queensland's east coast. Effective effort directed at the scallop stock has increased by a factor of fourteen in the period between 1977 and 1987. During this period, total annual catch increased from a base of 380 tonnes of meat to a peak of 1220 tonnes in 1982, then declined to 450 tonnes in 1987. Catch rates have fallen steadily between 1977 and 1987. Recruitment overfishing has been considered as a possible cause in the fishery's decline. Selective protection of broodstock may be an effective means of managing the scallop stock, as an alternative to restricting effort or actively enhancing the stock.

Key Words: Scallops, *Amusium japonicum balloti*, catch statistics, multi-species fishery, recruitment overfishing, broodstock protection

INTRODUCTION

A fishery for the scallop *Amusium japonicum balloti* Bernardi developed off the coast of southern and central Queensland (Australia) in the mid 1950s. The fishery is based in waters of the Great Barrier Reef Lagoon between 22°S and 26°S, in grounds which cover some 16000 km^2. Intermittent catches of scallops are made between 18°S and 21°S (Figure 1), and the species also supports a fishery in waters off Western Australia, between 25°S and 30°S (Heald and Caputi 1980). Scallops are normally trawled from depths of between 25 and 55 m, but have been recorded in depths between 10 and 75 m. A smaller sympatric species, *Amusium pleuronectes* L. occurs in shallow waters (<20 m) throughout the Indo-Pacific region and is fished with varying intensity by Australian and Asian fishermen.

The Queensland scallop fishery is one component of a complex multi-species otter trawl fishery which is largely managed as an entity. The status of the scallop stock will be examined in the light of this management regime.

The Trawler Fleet

Some 1140 otter trawlers are licensed to operate along the 2400 km of Queensland's eastern seaboard (Anon 1987). They fish for a range of shellfish stocks, including penaeid prawns (*Penaeidea*), slipper lobsters (*Scyllaridae*), portunid crabs (*Portunidae*), and scallops. In northern coastal waters, there is a mixed species fishery for tiger and endeavour prawn (*Penaeus esculentus, P. semisulcatus* and *Metapenaeus endeavouri, M. ensis*) and an irregular day time fishery for banana prawns (*P. merguiensis*). Waters of the Great Barrier Reef Lagoon support fisheries for king prawns (*P. longistylus* and *P. latisulcatus*) in addition to scallops. In southern waters, stocks of *P. esculentus*, a third species of king prawn (*P. plebejus*) and two *Metapenaeus* species also support fisheries. Slipper lobsters (*Thenus spp.*) and portunid crabs (*Portunus spp.*) are taken as marketable bycatch in all of these fisheries.

Most licensed trawlers have access to all of these stocks. Vessel design has been based on the need to evolve a small to medium size general purpose coastal trawler, equipped to handle a relatively low volume, high value catch, and have an extended range. Most vessels are between 10 and 20 m long (average 16 m), powered by diesel engines between 50 and 300 kw, and carry a comprehensive range of electronics, including 50 and 200 kz echo sounders, radar and multi range radio. Sonar is becoming widely accepted. A large proportion of the fleet operates in remote northern waters and may be at sea for periods of three months or more. Trawlers which fish in this area are equipped with snap freezing facilities which have the capacity to freeze one to two tons of wet product per day down to −40°C.

A major development in the fleet occurred between 1976 and 1978, at which time all boats towed two trawl nets spread by four otter boards. By substituting the inner boards for passive skids, fishermen were able to fit a third trawl net between the skids. The reduction in drag induced through the reduction to two boards outweighed the increase due to the extra net, and there was a rapid increase in the size of nets used in the fishery. A variant of this system, whereby four or six nets separated by skids and spread by four trawl boards, was utilized by many trawlers. In 1976, a trawler of average size and power typically towed two trawls with a combined head rope length of between 25 and 30 m. The same boat presently trawls with a combined headrope length of about 50 to 55 m.

In 1979, the previous open entry policy was reversed, and trawler numbers in the fleet were restricted to a total of 1270 vessels (Hill and Pashen 1985). There has been a slight reduction in numbers since that time. A number of regulatory measures including restrictions on net sizes, seasonal and area closures, designed to restrict growth of effective fishing power, have also been introduced since 1979. But improved gear technology and willingness by fishermen to spend more time at sea have negated these attempts to restrict the growth of effective fishing effort.

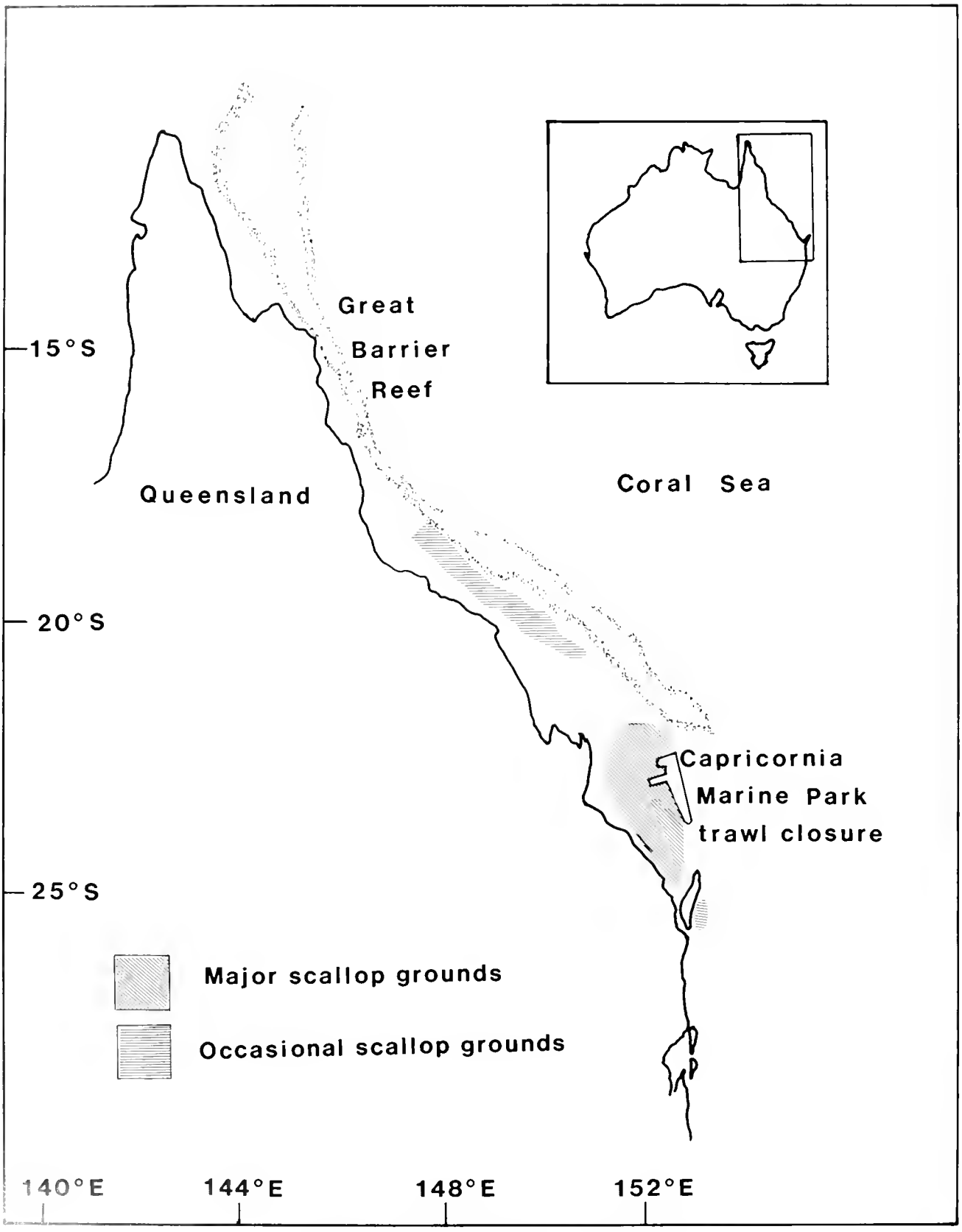

Figure 1. Location of scallop grounds off the Queensland coast.

The Scallop Fishery

Scallops occur in beds with maximum density of about one per m^2. Beds are separated by areas of low or zero scallop abundance. Fishermen working for scallops spend a certain amount of time searching for suitable concentrations if other vessels are not already working a bed. Once fishing has begun, trawlers will work continuously for periods of up to twelve days before returning to port. Trawlers fishing for scallops normally tow three nets at a speed of 3.6 to 4.4 km $hour^{-1}$. Trawl shots are of 1 to 3 hours duration. Scallops are held as whole animals on board, either frozen or refrigerated in a recirculated chill brine spray. Shucking takes place in onshore factories or moored processing barges, where the roe-off meat is frozen into block form or packed for the retail trade. Approximately 80% of Queensland's scallop production is exported, most going to Asia.

Scallop fisheries are characterized by irregular landings (Serchuk et al. 1979), but the extent of variability from the Queensland stock has been exceptional (Figure 2). Following an extended developmental phase between 1955 and 1968, landings followed an upward trend for some five years. Then followed a period of irregular highs and lows over a period of some 10 years, up to 1983. Between 1983 and 1986, total landings were reasonably stable. The appreciable decline recorded in 1987 may be significant.

There are no administrative or logistic barriers which restrict the entry of licensed Queensland trawlers into the scallop fishery. In 1980 only 20 trawler operators considered scallops to be their primary source of income, although more than 100 participated in the fishery, treating scallops as a secondary source of income after prawns (Williams 1980). Dredge (1985b) suggested that there was more than adequate fishing capacity to harvest the scallop stock. The availability of alternative stocks for trawlers to work should dampen earnings fluctuations in an environment where most fished species were short lived and showed irregular recruitment.

Excessive fishing effort has induced measurable reduction of recruitment in short lived tropical shellfish species. Multi-species fisheries are more at risk than those which are mono-specific (Penn and Caputi 1986). When there is appreciable environmentally induced variation in recruitment strength, the relationship between spawning stock size and recruitment may be extremely difficult to identify (Garcia and Le Reste 1981). But in heavily exploited stocks, the significance of stock depletion cannot be overlooked. In this paper, a description of the biology, fishery and known population parameters of *A. japonicum balloti* are given. The status of the stock is reviewed against a background of increased available fishing effort which can target on the species.

MATERIALS AND METHODS

Scallop Biology

An investigation aimed at describing the natural history of *A. japonicum balloti* and identifying sources of landing

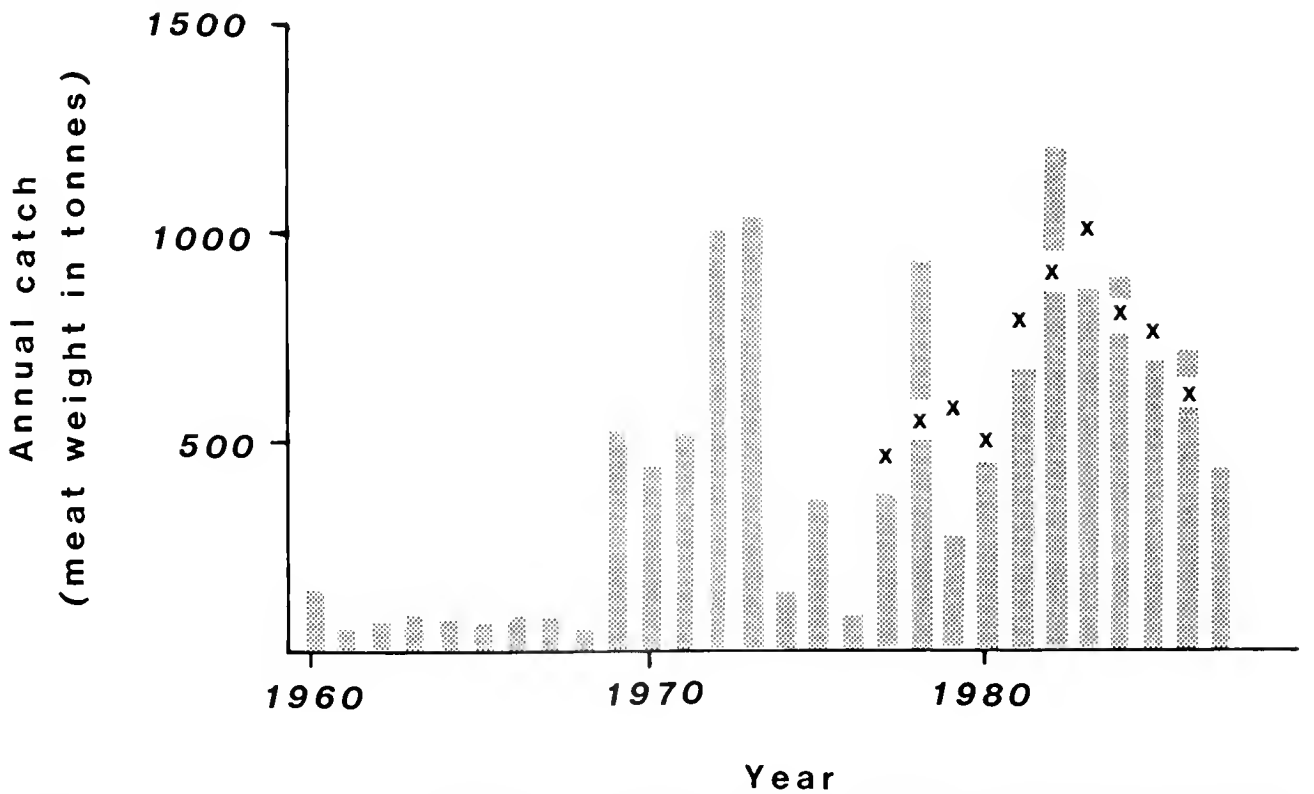

Figure 2. Annual landings of scallop from the Queensland fishery. Crosses indicate 3 year running averages of landings between 1976 and 1987.

variability was carried out in the period between 1976 and 1982.

Biological information was collected during a two year long monthly sampling programme on fished beds of *A. japonicum balloti*. In this programme, abundance, size composition, condition of the adductor muscle and reproductive status of scallops were monitored. An extensive tagging programme was undertaken to monitor growth, mortality and movement in the species. The growth and natural mortality parameters of scallops from an isolated bed were monitored in a second monthly sampling programme. Details of these programmes are given in Dredge (1981), Williams and Dredge (1981) and Dredge (1985a).

Catch and Effort Data

Information on the fishery was obtained by collecting both processor's landing figures, and detailed catch and effort data from fishermen. Processor's landing figures were summarized as total monthly landings. As all scallop processing works were monitored between 1976 and 1981, these figures are believed to be reliable estimates of total catch. Fishermen kept detailed (trawl by trawl) records of scallop and other catch on a voluntary basis. Data collected included catch weight by species, fishing location in 10 by 10 minute grids, time trawled, and depth. A separate file on each trawler's hull, engine and gear characteristics was maintained. Between 1976 and 1980, an average of 56% of total annual scallop landings were covered in this programme. The proportion of detailed catch and effort records declined to approximately 5% of total catch between 1981 and 1986 as the programme was wound down. Both the logbook and processors monitoring programmes were re-established in 1987 in response to reports of declining catch rates. Detailed catch rate and effort distribution statistics are available for approximately 14% of scallop catches taken since January 1987.

RESULTS

Scallop Biology

Amusium japonicum balloti spawned in winter and spring. Spawning coincided with temperature changing through the range of 18°C to 23°C. Mature females carried between 5×10^5 and 2×10^6 mature oocytes, and possibly spawned more than once in a single season (Dredge 1981). In laboratory conditions, a larval period of 18 to 22 days preceded settlement. There is some doubt as to the occurrence of a byssal phase (Rose and Campbell in press, Kettle 1984). Both tagging data and size frequency analysis showed that growth of juveniles was rapid. In 6 to 8 months, most scallops had attained a shell height of 85 mm, recruiting into the fishery at this size (Williams and Dredge 1981, Dredge 1985a). Sexual maturity was first reached at an age of one year or less and the natural mortality rate of adults ($M = 0.020–0.025$ week^{-1}) suggested that few animals survived longer than three years. A yield per recruit analysis indicated that yield would be maximized over a wide range of fishing mortality if the size of scallops at first capture was between 85 and 90 mm (Dredge 1985c).

Catch and Effort Data

Estimated annual landings and annual abundance indices based on catch rates but corrected to allow for increases in gear size are given in Table 1. The observed changes in catch rates covers the period 1976–1978, when unfished grounds south of 22°S were first being fished. By 1980 all grounds between 22°S and 26°S were searched comprehensively each year (Figure 3). New grounds north of 22°S are still being identified. In previously unfished areas, beds of scallops containing animals from more than one year class were found. Such beds were highly productive.

Total effort directed at the scallop stock has been estimated by dividing estimates of total catch by average catch rate (Table 1). In the period between 1976 and 1987, trawlers doubled their effective fishing power on the basis of increase in net size alone. The sharp increase in boat hours trawled is amplified by this increase in net size. The decline in catch rate between 1978 and 1980 corresponds to the period when grounds were considered to be fully exploited, with beds being dominated by single age classes. The second decline in catch rates (1984–5) coincided with an substantial shift in scallop meat price (Table 2), which encouraged fishermen to keep trawling at extremely low scallop densities.

Stock and Recruitment

With the exception of unfished scallops in the Capricornia section of the Great Barrier Reef Marine Park (Figure 1), survivors from one year class (the late 0+ and

TABLE 1.

Annual catch, standardised catch rate, estimated effort expenditure and average net size for the scallop fishery.

Year	Total catch (tonnes of adductor meat)	Mean catch rate per m head rope (kgs/hour)	Boat hours trawled	Average trawl headrope length (m)
1976	70	0.85	3000	25
1977	380	1.44	11000	25
1978	950	1.28	25000	30
1979	250	0.62	14000	30
1980	530	0.34	43000	36
1981	660	0.33	53000	36
1982	1220	0.38	86000	36
1983	880	0.66	38000	36
1984	900	0.30	81000	36
1985	660	0.13	107000	46
1986	700	0.13	116000	51
1987	450	0.11	77000	51

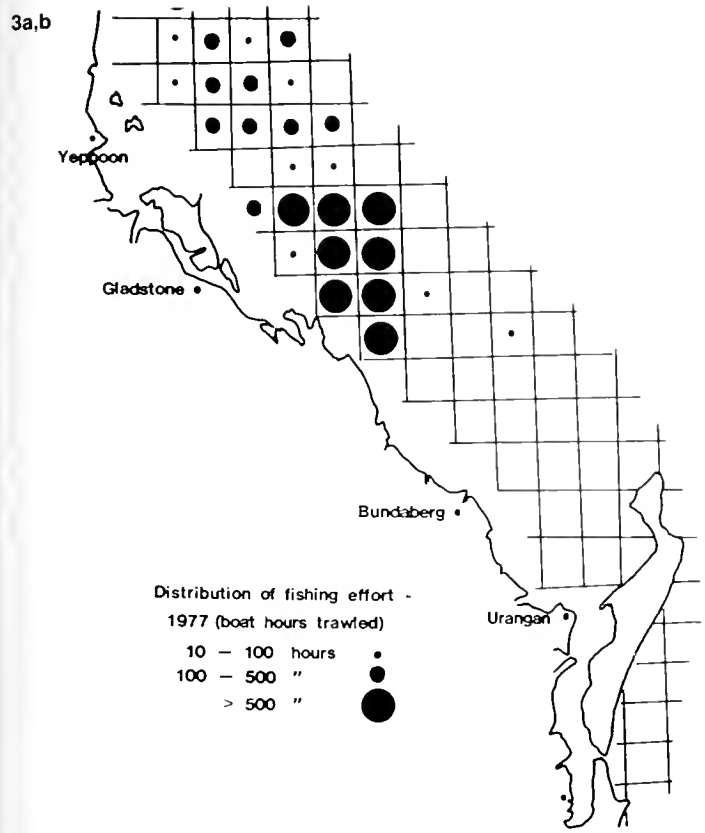

Figure 3a. Location of fishing effort-1977.

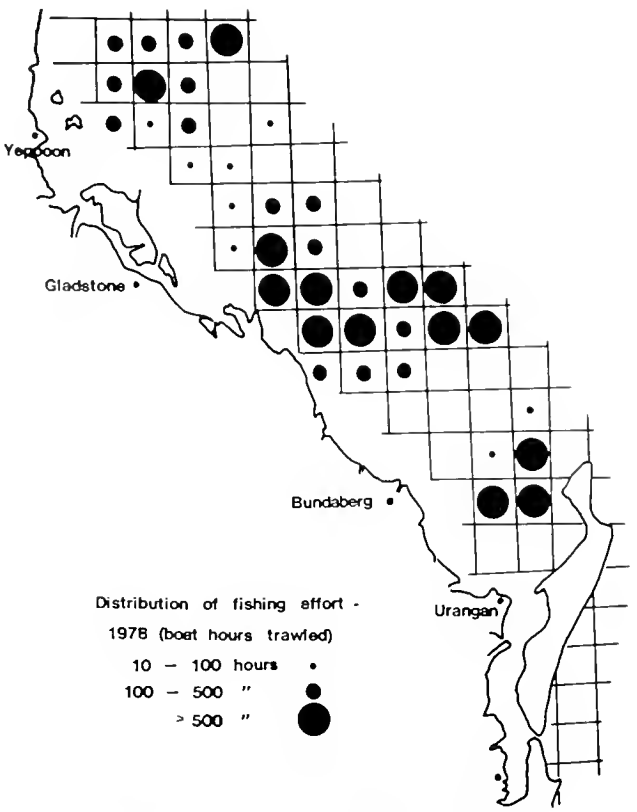

Figure 3b. Location of fishing effort-1978.

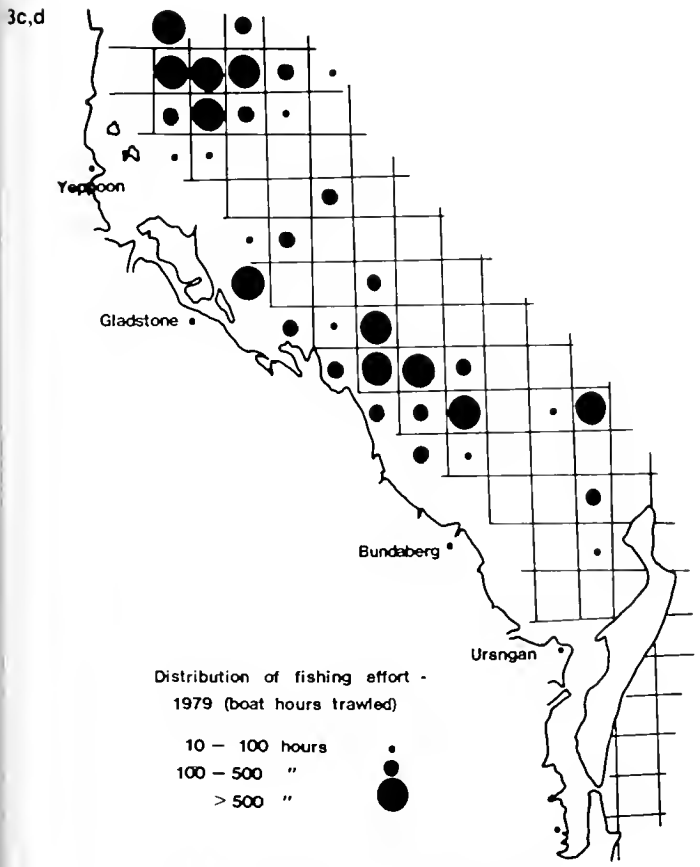

Figure 3c. Location of fishing effort-1979.

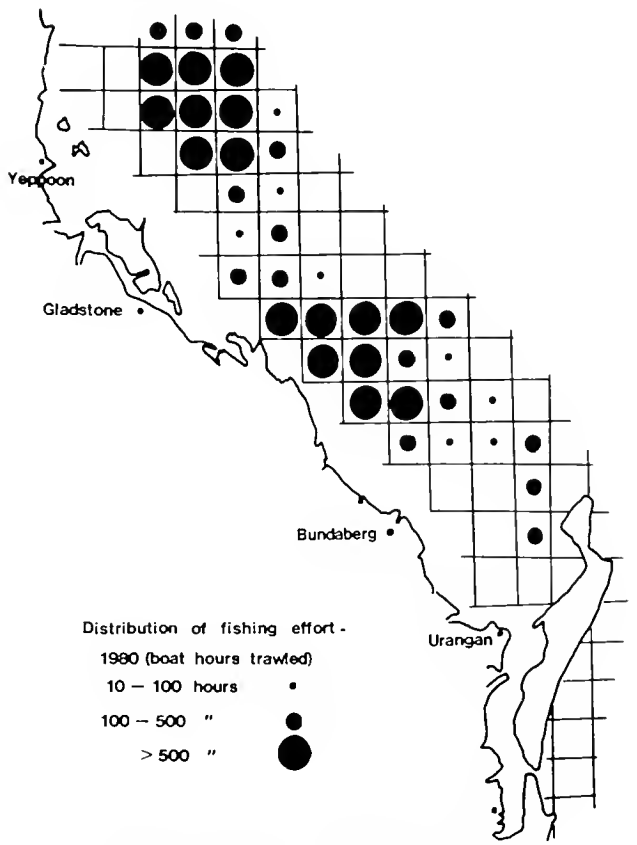

Figure 3d. Location of fishing effort-1980.

TABLE 2.

Average price paid to fishermen for scallop meat (110 meats/kg)*

Year	Price in $A/kg	Price indexed to 1980 $A	Price in $US
1980	5.87	5.87	6.81
1981	5.00	4.58	5.80
1982	6.00	4.99	6.61
1983	5.32	4.50	4.99
1984	7.87	5.59	7.13
1985	11.25	7.54	8.72
1986	16.30	8.41	11.22
1987	18.00	8.56	12.78

* Base source: Seito Ocean Products, Bundaberg, Queensland.

early 1+ group) are thought to make up the bulk of the catch and of spawners each year. The fishery is therefore dependent upon the success of this single year class for its continuity. There are insufficient data available to develop an accurate stock-recruitment relationship at this time.

DISCUSSION

The Queensland scallop fishery has developed rapidly in the period between 1976 and 1987. Between 1977 and 1982 an eight fold increase in boat hours trawled was accompanied by a doubling of annual landings. Effective effort continued to increase between 1982 and 1986, while annual landings declined from an unexplained high point in 1982.

In the three years between 1983 and 1986, there was sufficient available trawling effort directed at scallops to cover the total grounds between 22°S and 26°S between one and one and a half times each year. There is sufficient searching power in the fishery to locate virtually all scallop beds during the course of a year's trawling. Once a bed is discovered, it is ultimately reduced to a density at which fishing is no longer profitable. In 1986 and early 1987, the cut off point corresponded to a real scallop density of about one animal per 120 to 150 m^{-1}. This high level of efficiency means that the fishery is largely based upon late 0+ or early 1+ animals, depending on time of year. Few animals survive much longer than 18 months to 2 years. A yield per recruit analysis indicated that maximum yield would be obtained by first harvesting scallops at an age of 6–8 months (Dredge 1985c), which is the present situation in the fishery. But scallops from the single year class which now dominates the stock comprise the majority of spawners. As they are subject to heavy fishing pressure prior to spawning, as 0+ animals, the stability of future recruitment strength must be questioned.

The propensity of scallop stocks to vary greatly in numbers as functions of either undescribed or subtle causes is well known (Serchuck et al. 1979, Caddy 1979). But the massive increase in effort aimed at the Queensland stock of *A. japonicum balloti*, associated decline in catch rates and recent decline in total catch indicates that there may be a decline in recruitment as a consequence of excessive fishing pressure. Evidence that recruitment overfishing can occur in short lived tropical species has encouraged managers of Queensland's fisheries to adopt conservative management policies which include acceptance that recruitment overfishing may occur in scallop stocks, even though such overfishing may not have been conclusively proved.

No alteration to the present regime of open access to the scallop fishery has been considered. Previous consideration or implementation of limited entry in other Queensland fisheries has lead to an increase in fishing effort in the short term. This apparent contradiction has occurred because access to the limited fishery has been only available to those with a history of participation in the fishery. In the period between discussing limited entry and actual implementation, a great many fishermen manage to acquire some historic rights to the stock.

An alternative strategy to enforced effort restriction currently under consideration involves recruitment enhancement by selectively protecting broodstock. If a model of larval transport can be formulated, tested and verified, areas from which spat originate can be delineated. If adults in these areas were protected, reproductive potential of the stock should be enhanced.

Information on water transport in the Barrier Reef Lagoon between 22°S and 26°S is limited (Woodhead 1970, Griffin et al. 1987, Campbell unpub). Available data indicate that a gyre in Hervey Bay may act as a trap to larvae

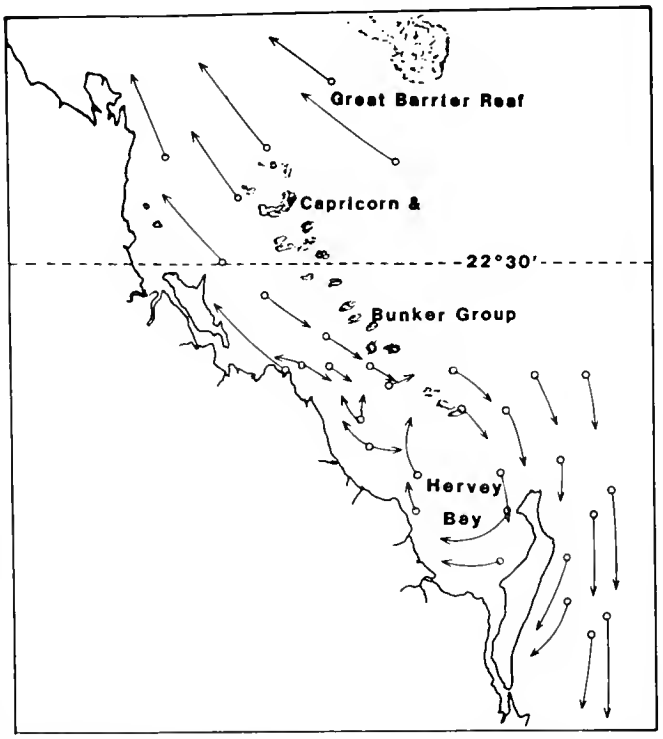

Figure 4. Summary of known surface water transport in the major scallop grounds.

spawned to the west of the Bunker and Capricorn groups of islands, whilst larvae produced near and to the east of these islands may be dispersed southward (Figure 4) to areas which do not normally support scallop fisheries. The only water transport model which can be used to model larval advection in the northern part of the stock's distribution suggests there may be net northwest transport (Griffin et al. 1987).

Knowledge of the early life history of *A. japonicum balloti* is limited. Before serious consideration could be given to managing the scallop stock by selective protection of broodstock, additional information on larval behavior and mortality is needed. Given that larval transport may not be entirely passive, the relationship between water transport and larval dispersion needs elucidation. Further information on fine scale timing of spawning is also essential for effective modelling of the system.

Stock enhancement by seeding out spat caught in conventional mesh bags for growout has also been considered. Pilot studies failed to demonstrate the validity of this technique (Sumpton pers. com.). The rearing of scallop seed in hatcheries has also been suggested as a means of stock enhancement, but could only be regarded as a long term option.

Taking steps to protect a stock before recruitment overfishing has been clearly demonstrated could be interpreted as an indication of panic or an imposition of unnecessary costs on the industry. But recent experiences in Australian peneaid prawn fisheries have clearly shown that the costs and social trauma associated with rehabilitating overfished and overcapitalized fisheries (Kailis 1985) far outweigh the small benefit gained by allowing a stock to be exploited to a point where recruitment overfishing can be clearly recognised.

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SHELLFISH CULTIVATION AND FISHERY BEFORE AND AFTER A MAJOR FLOOD BARRIER CONSTRUCTION PROJECT IN THE SOUTHWESTERN NETHERLANDS

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ABSTRACT After a disastrous flood in 1953, a law was passed to close the mouths of all estuaries but one in the Southwest of the Netherlands. The estuaries concerned were planned to become fresh water lakes. Existing bottom culture of the blue mussel (*Mytilus edulis*) and the European flat oyster (*Ostrea edulis*) as well as finfish and shrimp fisheries were to disappear from the area. After a change in national politics and intensive lobbying by nature conservation and fishery organizations, this plan was modified in such a way that a restricted tidal movement would remain possible in the main estuary, the Oosterschelde (Eastern Scheldt). Besides, good ecological conditions in another estuary already shut off from the sea, prompted the decision to conserve this area as a tideless marine lake. These decisions gave new hopes for the aquaculture and fishing industry. Although many of the existing shellfish cultivation plots had to be abandoned, also new possibilities have become apparent, such as the emerging of a natural population of the European flat oyster in stagnant Lake Grevelingen. Besides, new chances for bottom cultivation of mussels and oysters have become apparent in places where tidal current velocities have been reduced. Limits to shellfish culture and fishery can be set by locally too low current velocities and by food limitation due to competition or a reduced import of suspended matter from the North Sea. Phytoplankton production might also become limited as a result of reduced import of nutrients by rivers.

Research is under way to assess new possibilities for aquaculture to predict possible effects of the project on environment and mariculture in the area. Management of aquaculture and fishery is facing the problems of compensating for lost cultivating plots, allotment of new ones and conflicts of interest between different cultures and fisheries.

KEY WORDS: Culture of oysters, mussels, *Ostrea edulis*, *Mytilus edulis*, Bottom cultivation, Flood barrier construction, Fishery management

1. PROLOGUE: A STORM FLOOD AND ITS AFTERMATH, THE DELTA PLAN

The long-standing reputation of the Dutch as land reclaimers and hydraulic engineers is built on a centuries-long series of battles against the sea. Most of these battles were won but, in many cases, it was the defeats which gave the spur to efforts which led to the next victory. In this way, the Low Countries have, in the course of the last centuries, created a protection from floods by means of a girdle of dikes. This dike system, however, had frequently to be repaired when storms or currents had damaged it, or heightened when necessary. Also the need of the population for new farmland prompted, until some years ago, new land reclamations. But there are periods when money is short and local and central governments not able or motivated to do much about the upkeep of the dikes. This was the case during the first half of this century, when successively the first world war, the economic crisis and the second world war had distracted money and attention from the maintenance of this vital defense against the sea. Most of the sea dikes of the country were too low to match the effects of a steadily subsiding soil and rising of the sea level. Also many dikes were in a poor state of repair. Still to the astonishment of many, on the night of the first of February 1953, a fatal combination of spring tide, a force 13 storm and shifting wind direction pushed up the sea water in the southern North Sea. The shifting wind drove the flood high up into the estuaries in the southeast of the Netherlands. Water levels of 3 m above the normal spring flood level were reached. On many places the dikes broke through and a total area of 250,000 ha (600,000 acres) was flooded. Over one thousand eight hundred people died and thousands of head of cattle drowned. This catastrophe prompted the adoption of a law in 1958, aimed at safeguarding the protection of the coastline in the Southwestern Netherlands. The law comprised a scheme called the "Delta Plan", which encompassed the closure of all southern estuaries, except the Westerschelde (Western Scheldt), which is the waterway to the large seaport of Antwerpen. The strategy of the plan was to straighten the coastline, thus decreasing the length of the sea-defense line with 700 km. For instance, a dam in the Oosterschelde with a length of 9 km would replace 245 kms of dike. Besides, the plan aimed at increasing the height of the sea-dikes in such a way that the risk of a storm flooding was brought down to 1 : 4,000.

2. BENEFITS AND DISADVANTAGES OF THE PLAN

The benefits of this plan were obvious: On a national level, security would be guaranteed, for the many islands in the Delta area the plan would also end a centuries-long isolation and lead the way to further development. Opportunities would arise for industrial development in a province which before had been based on agriculture and fishery. Agriculture, in its turn, would benefit from the fresh water which was planned to surround the islands. Salt water intrusion would be stopped in important horticultural and agricultural regions, which would make the production of an

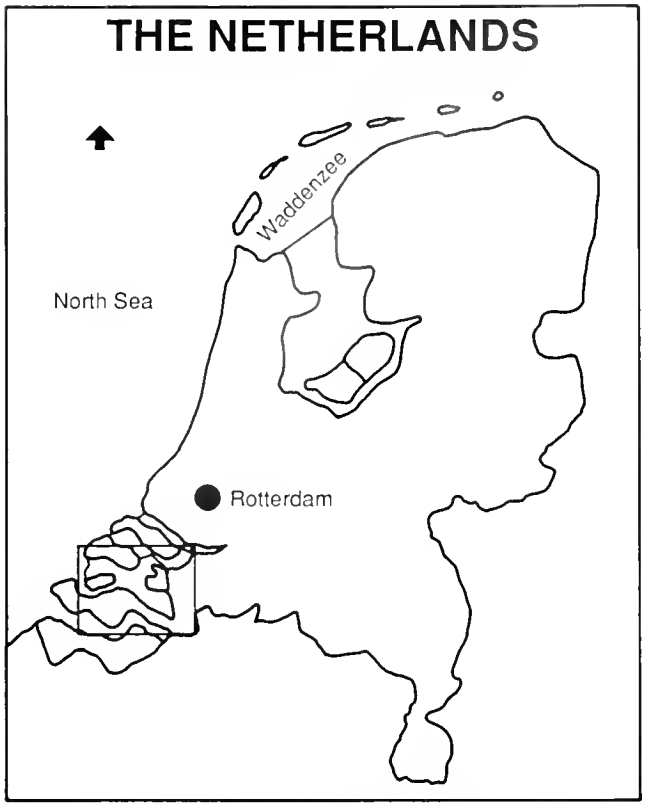

Figure 1. General view of the Netherlands, showing the Delta region and the Waddenzee.

assortment of new crops possible. But it was realised also that there would be disadvantages, notably to fishery and mariculture. A commission was installed to assess the total economic damage to these industries and to the trade and industry branches dependent on them. Even the impact on the national import and export balance was studied. The total damage to all fisheries and aquaculture was, in 1955, estimated 142 millions of Dutch guilders (one guilder is about US$ 0.50). In these days this would mean the relatively modest amount of 619 millions of guilders. Figure 2 shows the locations where mariculture was carried out before the Delta Plan. A series of compensating and mitigating actions were necessary.

Oyster culture, which was practised exclusively in the Delta waters, would disappear. As no alternative locations existed, the entire industry, about 100 companies among which 15 large ones, would have to be compensated, which would cost 40 millions of guilders. In 1962–1963, an extraordinarily cold winter destroyed most of the cultivation installations and decimated the stock of cultivated oysters. Although the closure of the Oosterschelde was not due yet, the government decided to anticipate the compensation of the oyster industry, as re-building of the industry for such a short period had little sense. All but 10 of the 100 oyster farmers were bought out and terminated their activities. The ten that remained, which had also other means of existence and hence were less dependent on oyster culture alone, were indemnised as well. They were allowed to remain in business as long as this was still possible, but had no right to claim any damages. The other ninety, whose sole occupation was oyster farming, found other professions or retired. This development gave rise to the establishment of a number of mushroom and poultry farms in the neighbourhood of the township of Yerseke, the center of the shellfish industry in Zeeland, situated in the southeastern part of the Oosterschelde (figure. 1) Mussel cultivation, as far as carried out in the Delta area, would have to disappear and be moved to the Waddenzee in the North of the country, where new cultivation grounds should have to be sought. More than half of the mussel cultivation was already being practised in that area. For reasons of risk-spreading, most mussel farmers rented plots in the more sheltered southern estuaries as well as in the productive, but exposed and hence risky Waddenzee. This meant that for most of them the change was not too drastic, but that the risk of storm and ice damage in winter would increase. The first mussel culturists to lose their plots in the Delta region were those from the Zandkreek and the Grevelingen. (figure 3). Many of them could be allotted plots in other areas, others stopped mussel farming and took to other professions like fishing eels with fyke nets, which fishery was expected to be profitable in the future fresh lakes. Another aspect was the trade and processing of mussels. The entire Dutch mussel production, including that from the Waddenzee, (about 100,000 tons per year) is processed and packed in and around Yerseke. A vital stage in mussel processing is the purification or "rewatering", a compulsory re-laying period of minimally 10 days in quiet, clear and bacteriologically pure seawater within the tidal range. This stage is necessary to eliminate dead and crushed mussels, to enable the mussels to dispose of sand and silt and to give them the shelf life and sanitary quality which is required for export. The only location where these requirements can be met is situated close to Yerseke in the Oosterschelde. Rewatering in the Waddenzee is impossible because of a high turbidity of the water and a limited tidal range. An installation would have to be designed to do this artifically. The Netherlands Institute for Fishery Investigations was given the assignment to develop this process in a pilot-plant and to make a blueprint for a definitive installation, big enough to process the entire Dutch mussel production. To this end the Mussel Experimental Station of the Netherlands Institute for Fishery Investigations was built in 1969 on the Waddenzee island of Texel. This was in operation until 1979, when the laboratory was moved back to the Delta region and was established in Yerseke. Also the inshore fishermen would lose their fishing grounds and jobs or would have to accept lower incomes due to the Delta Plan. Likewise would the fish traders and exporters, as most of the catches were destined to foreign markets like Belgium, France or Germany. This trade comprised a variety of species like shrimps, lobsters (locally captured or imported

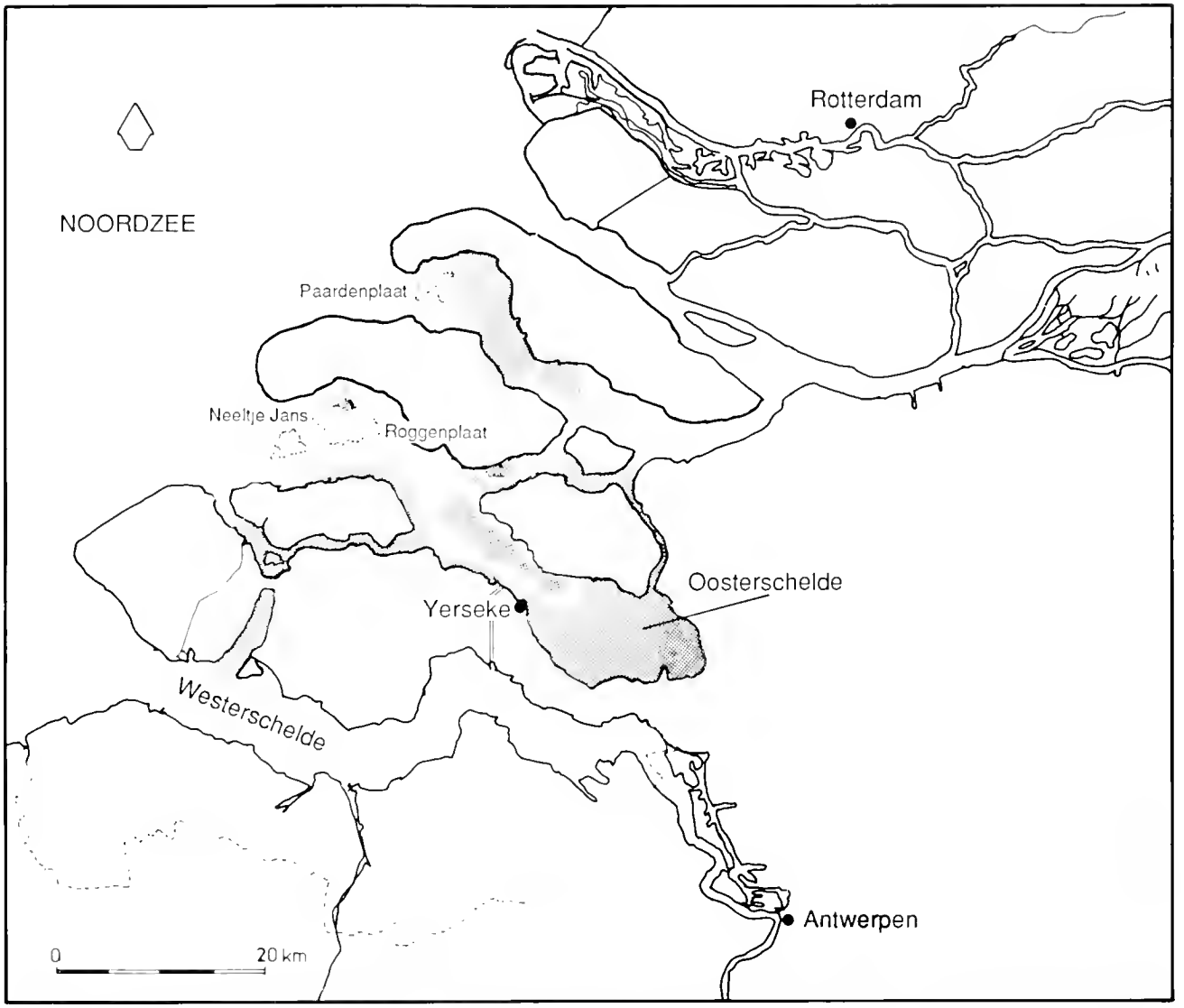

Figure 2. The areas in the Delta region (hatched) where mussels and oysters were cultivated before the start of the Delta plan in 1963.

and stored in in- or outdoor ponds), crabs, periwinkles, whelks and even starfish, which by that time were used for soil improvement in agriculture. Another problem would arise for the North Sea fishermen from the township of Veere. The closure of the sea-arm to that harbour was due in 1961, which meant that the fishermen were obliged to have their ships removed by that time. Some decades earlier, the same had happened with the nearby port of Arnemuiden, from which many fishermen had moved to Veere. For the second time they had to change the registration numbers on the bows of their ships, when a new harbour was created for them in the village of Colijnsplaat at the Oosterschelde. This time it would also mean a provisional removal, as the Oosterschelde was scheduled to be closed off by 1978 and no shiplock was foreseen in the dam. This migration of fishermen and their families created a new aspect: a fishermen's community within the hitherto exclusively agricultural village of Colijnsplaat. Fishery research had demonstrated that the estuaries of the Delta region, with their large areas of sandflats and shoals, form the nursery area where a part of the commercial fish and shrimp stocks pass their first years of life before they migrate to the deeper waters where they are captured. As the fish species concerned: shrimps, plaice, dab and common sole, make out a substantial part of the catches of the coastal fishing fleet, elimination of these nursery zones would have a direct negative impact on fishery. Furthermore, the rocky bottom, created by the stones used for reinforcement of the underwater part of the dike-slopes, makes a suitable environment for many species which normally do not occur at the sandy and muddy coasts between Dover Strait and Norway. Also the relatively high water temperatures in the inland part of the Oosterschelde during summer (up to 24 degrees C) make reproduction possible

for a number of species the occurrence of which would otherwise be restricted to warmer waters south of Dover Strait. Also evidence was supplied that the Delta region has a vital importance as a foraging area for thousands of migrating and wintering birds, whose safe arrival in their areas of destination often depends on foraging possibilities during the voyage. The vast intertidal area (a tidal range of about 3.5 m) offered unique feeding grounds for more than 400,000 wading birds, geese and ducks simultaneously. This makes the Delta area second in importance among the European areas for migrating birds. It has also been the main argument to grant the area the official international status as "wetland". Elimination of the tidal zone and creation of fresh water lakes would cause problems for bird populations, breeding in a number of countries.

3. GROWING OPPOSITION AND TURN-AROUND

The first decade after the disaster, most of the attention was understandably aimed at safety aspects. Gradually, a number of persons became aware that the price to be paid for safety would be higher than the costs alone of the plan sketched above. Initially one, later more members of parliament opposed the chosen solution. As said, the arguments for this opposition came in first instance from the fishing and aquaculture industry. Only in a later stage, more attention was paid to the damage, done to the natural environment of the Delta region. This was mainly due to the fact that a public awareness of the importance of nature conservation was just starting to grow by that time. The recent loss of a number of areas of great natural value in behalf of public safety and industrial development and the awareness that the Grevelingen and the Veerse Meer were already lost as tidal areas, gave rise to a growing opposition against closure of the Oosterschelde. Opponents were convinced that the promise of safety, done to the populace of the affected provinces had precluded a proper weighing of arguments in the discussion about whether the Oosterschelde had to remain a tidal water or not. The arguments in favour of nature conservation, fishery and aquaculture had not received, they argued, the attention they deserved. They advocated heightening of the dikes around the Oosterschelde, thus leaving the tidal movement undisturbed. This alternative was contested by representatives of agriculture, water authorities and some conservative politicians, who either wanted fresh water, or just did not want to change the original plans, saying that the alternative was irrealistic. The opponents to closure demanded the installation of an independent commission, comprising experts of all disciplines concerned, which should give advice to the government about which alternative should have to be chosen. In the final stage of the battle, some sixteen national associations of fishermen, aquaculturists and nature conservationists took action, first all on their own, later unitedly. Scientific articles about the natural values of the estuary and the detrimental effects of closure were written, conferences were held about the nature and fishery function of the estuary and all over the province the slogan "Oosterschelde open!" was chalked down in huge characters. Many of the actions were private, others were financed by the industry. The most important aim was, of course, to persuade as many members of parliament as possible, because only in parliament the Delta Plan, which had become law, could be modified. Finally, after many actions and much lobbying, parliament decided, in 1974, to install an independent commission, which should bring out an advice about what to do with the Oosterschelde. This was just in time. The other sea arms had been closed off already, and the preparations for the closure of the Oosterschelde were already in full swing. Six months later, the commission chose the alternative in which the Oosterschelde would be closed with a permeable dam. The tidal flow through that dam had, according to the Commission, to be sufficient to conserve the tidal character of the Oosterschelde and to leave the marine aquatic environment intact, so that the natural value, the fishery and aquaculture should not be affected. To guarantee a sufficient salinity and water quality, two secondary dams would have to be made, in addition to the barrier in the mouth of the Oosterschelde. Primary in this advice stood the interest of nature conservation, the interests of fishery and agriculture came second. Least in importance was considered the interest of recreation, which was becoming an important source of income in many parts of the province, but also was considered as a threat for nature and shellfish cultures. In 1976, Government adopted the advice of the commission and as soon as possible preparations were started for the construction of the permeable dam. As completion of this dam was only expected after at least eight years, all dikes had to be heightened to provide sufficient safety during the period of construction. This can be considered as a concession, made to those politicians who clung to the promise of safety, done to the population and did not want to delay the closure. This turn-around in Government policy was considered a major victory, especially for nature conservationists. That it was possible to change this new law was mainly due to the fact that in the meantime the socialist party had obtained a majority in government, which resulted in an increased awareness of the necessity of nature conservation. Additionally, the financial barriers (the solution chosen would cost 1.6 billions of guilders more than total closure) were taken away mainly thanks to the discovery of huge reserves of natural gas, which substantially alleviated the national financial position. The total costs of the project were then estimated 5 billions of guilders. The final costs appeared to have been 7.8 billions, mainly due to inflation. It is generally acknowledged now, that otherwise the Oosterschelde would have been closed. How narrow the escape was, is illustrated by the fact that the name chosen for the planned fresh-water Oosterschelde: "Zeeuwse Meer" (Lake Zeeland) can nowadays still be found on certain maps.

4. THE FINAL SHAPE OF THE DELTA PROJECT

Construction of a barrier in the mouth of Oosterschelde would inevitably bring about a reduction of the tidal flow and of the tidal range inthe estuary. If this reduction should be too large, problems would arise for the natural environment as well as for fisheries and aquaculture. The commission has realised this, and formulated the requirements for the future tidal range. A technical commission formulated three alternative sizes for the aperture in the Storm Surge Barrier, as it was named, in the Oosterschelde. Finally, an aperture of 14,000 m2 was chosen, which would cause a reduction of the tidal current by 25% and of the tidal volume by 35%. The tidal volume, the mass of water, changed each tide, was to be 1,600 million cubic meters. The tidal range at the location of the mussel rewatering plots off Yerseke would decrease from 3.5 m to 2.7 m, considered sufficient for the mussel cutters to navigate and to fish on the plots. The rate of tidal flushing of the estuary would, if a greater reduction of the aperture should be chosen, be insufficient to maintain a good salinity in the estuary. Figure 3 shows the situation after completion of the Delta project.

The "Compartmentating Dams"

Two secundary dams: the Oesterdam in the southeast of the Oosterschelde and the Philipsdam in its northern branch (figure 3), served three purposes: In the first place they had to decrease the tidal volume and thus to alleviate the current speeds in the barrier. Second, they had to conduct the fresh water, coming from several rivers to the Westerchelde, because otherwise the salinity exigencies for the Oosterschelde, set by the tolerance limits of oysters and lobsters, would not be met. In the third place, the dams were to protect a tide-free waterway between the ports of Antwerpen and Rotterdam, a result of an earlier agreement between the Dutch and Belgian governments. In all dams shiplocks were planned. In the Philipsdam, where the locking of ships would cause intrusion of fresh water into the Oosterschelde and that of salt water in the future fresh water lake, an ingenious system was made to keep fresh and salt water separated during the operation of locking up or down the ships. This system is based on the floating of fresh water on top of sea water.

The Haringvliet

The former estuary of the river Meuse, the Haringvliet, in the north of the Delta area, was closed off with a storm barrier in 1968. Apart from providing safety, the dam holds the salt tongue in the estuary in check, thus protecting a very important horticultural area. The resulting fresh water lake now knows a profitable fishery, mainly on eels.

Lake Veere (Veerse Meer)

This was the easiest and for this reason the first sea arm to be closed off in the project, in 1961. The water in this lake is brackish due to freshwater discharges from the surrounding farmland. The mean salinity is about 15–20 parts per thousand. Several mussel and oyster plots had to disappear after the closure of this lake. The aquatic flora and fauna have impoverished considerably, and only a thriving eel fishery is now practised on the lake. Water authorities consider raising the salinity by flushing with water from the sea or the Oosterschelde. This would create new opportunities, at least for oyster culture.

The Zoommeer

This fresh water lake, or rather a string of lakes and waterways, is left between the mainland and the secondary dams in the east of the Delta region. It came into existence when in April 1987 the Philipsdam, as last compartmentating dam, was closed. To speed up the freshening process and avoid a cumbersome period with brackish water, stratification and mass mortalities during the ensuing summer, it was decided to flush the lake with water from the northern rivers. Due to the presence of some small rivers and the salt/freshwater separation system in the shiplocks, the lake will eventually become totally fresh. The first results of eel fishery appear favourable, spontaneous colonisation with other fresh water fishes like roach, perch and pike-perch has started. The consequences of this part of the project for oyster cultivation are not as favourable, the fresh lake now covers a number of former oyster growing plots.

5. THE SURPRISE OF LAKE GREVELINGEN

In 1964 the Grevelingen estuary had been closed at the landward side with a dam. In May 1971, a second dam was completed, which meant that the estuary had become a lake, still filled with sea water. The intention was to leave the lake in that state until fresh water would be available in the adjacent sea arm. All cultivation of mussels and oysters had been stopped and the salt water lake was considered lost, doomed to become a brackish, stagnant and stratificated pool. This feeling was strengthened by the mortality among bottom organisms immediately following the closure.

Apparently the sudden ceasing of tidal movement had caused an ecological change to which many of these organisms were not adapted. In the following years, however, aquatic flora and fauna revived, although not without considerable changes in composition. Particularly those species were favoured which reproduce with large numbers of pelagic larvae, which no longer were dispersed into the open sea and diluted by tidal currents. A series of excessively abundant year classes of such species followed. First came an explosion of the blue mussel (*Mytilus edulis*) in the period 1974–1980. In 1980 the stock of mussels was assessed at 22,000 tons fresh weight. The shells of mussels which had died during a period of stratification gave rise to a birth explosion of the European flat oyster (*Ostrea edulis* L) by offering substrate for settlement. In the meantime,

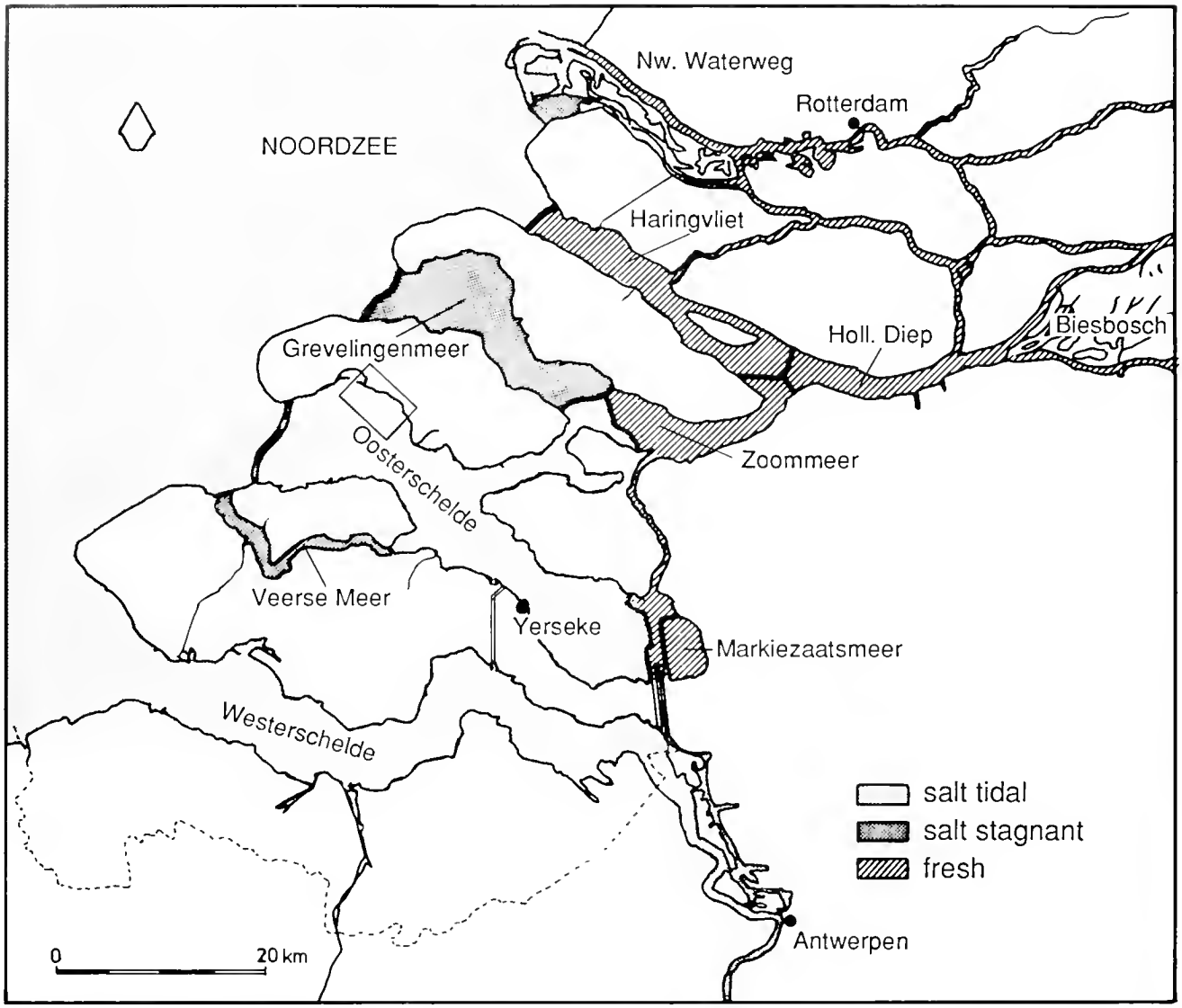

Figure 3. The Delta region in 1987 with –numbered– the different closure dams: 1: Zandkreekdam, 2: Veerse Gat dam, 3: Grevelingendam, 4: Volkerakdam, 5: Haringvliet Barrier, 6: Brouwersdam, 7: Oosterschelde Storm Surge Barrier, 8: Philipsdam, 9: Oesterdam. Different salinities and tidal regimes are indicated. The water in the Veerse Meer is brackish (vide text). The framed area in the Oosterschelde is the area, meant in fig. 6.

large yearclasses of the starfish *Asterias rubens L* and the shore crab (*Carcinus maenas*) occurred during the period 1981–1984. Between 1982 and 1985 meadows of the tunicate species *Cionia intestinalis* and *Ascidiella aspersa* covered particularly the deeper ranges of the lake and affected oyster culture by acting as competitors for space on spat collectors. Also the Netted Dog Whelk (*Nassarius reticulatus L*) occurred, especially during the last years, in densities, unknown from "normal" estuarine waters. It is supposed that the fluctuations in numbers of most organisms are stabilising somewhat during the last few years. A cause for such a stabilisation is, however, difficult to give. The flat oyster, on the other hand, showed a gradual increase in numbers, which started in 1975 and levelled off around 1985. This oyster stock originated from a small number of oysters, left over after the oyster farmers had fished clean their plots in 1964, when all aquaculture operations in the estuary ceased. These oysters had survived the very cold winter of 1962–1963, when water temperatures of minus 1.5 degree Celsius prevailed during several months in the ice-covered lake. They must have caused the rapid development of the oyster population, which was triggered by favourable water temperatures during the warm summer of 1976. The population kept on growing during the years to follow. After this oyster population was discovered, our institute embarked on an extensive program, to follow the development and distribution of the population and to obtain a view on settlement and development of the spat. Soon it appeared that Lake Grevelingen has outstanding qualities as breeding area for the flat oyster. Thanks to the

absence of tidal exchange, water temperatures rise rapidly in June, and temperatures above 20 degrees Centigrade prevail during several weeks almost every year. Concentrations of oyster larvae of over 20,000 larvae per cubic meter are regularly found with 2,000–4,000 as an average. Spatfall on mussel shells in the lake appeared to be profuse in most years, 20–30 spat on a mussel shell are no exception in the first week after settlement. Mortality of the newly-settled spat, however, is high. In June of the next year not more than 5–10% of the settled spat survived (Dijkema c.s., 1985) (Figure 4). This, however, appears to be sufficient to sustain the oyster population in the lake and to allow a yearly catch of 2–3 millions of wild oysters. Besides, some 10–12 millions of oysters were cultivated on an area of about 150 ha of cultivation plots. This area has been enlarged in 1987 until 380 ha. Plans to use the seed oyster production of Lake Grevelingen to repopulate the cultivation plots in the Oosterschelde, which had been in disuse since 1963, were frustrated by a new disaster: the outbreak of the oyster disease *Bonamia*, introduced from France in 1980, which made a total ban on oyster cultivation in the Oosterschelde necessary. This ban was only partially lifted in 1987, as still traces of *Bonamia* are being found in the area. This event made Lake Grevelingen the cork on which the Dutch oyster industry has been floating until this moment. Deprived of their plots in the Oosterschelde, the oyster growers and exporters could only serve the market with oysters from Lake Grevelingen. Fortunately, the decimation of the flat oyster stocks in Europe's most important producing countries: France and England and later also Ireland, have caused oyster prices to rise sharply, which slightly mitigates the low production. As the oyster disease has more or less been overcome, the Ministry of Agriculture and Fisheries has decided to create conditions for a rapid re-population of the derelict oyster

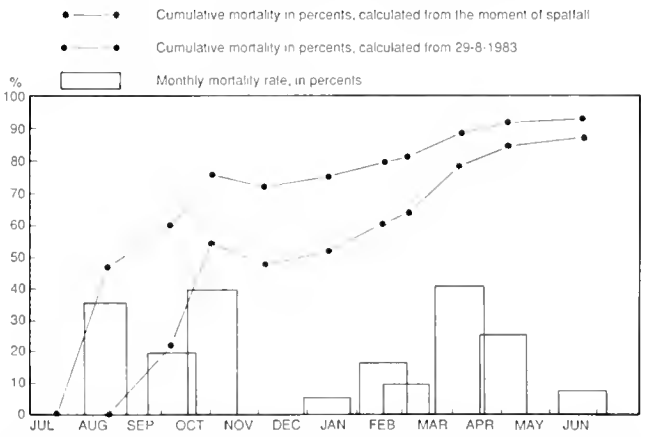

Figure 4. Cumulative mortality of oyster spat (*O. edulis*), starting on the moment of spatfall and on 29–8–1983 (line chart). The histogram represents the monthly mortality rate of the spat during its first year of life. The spat has settled on mussel shell cultch on a plot on the bottom of Lake Grevelingen, period July 1983–June 1984 (Dijkema c.s., 1985).

plots in the Oosterschelde. The basic aim is to use Lake Grevelingen for seed oyster production because of its favourable conditions for settlement, using the Oosterschelde plots (1,700 ha) for final fattening. This is because the ecological conditions in the Oosterschelde: higher current speeds and lower temperatures in summer, are more favourable for fattening. Probably due to the low current velocities in the lake, the shells of the oysters are thin, and can crumble when the oysters are opened. Another shell problem in the Shell Disease (*Ostracoblabe implexa*), which can cause considerable shell damage and mortality after warm summers. For this reason final fattening in the Oosterschelde, with a lower infection rate with shell disease, is preferred. This year an extension has been made of the cultivation and spat collecting plots in the lake from 150 to 500 ha. A possibility has been created for all practising Dutch oyster growers to lease plots, instead of the limited group that was allowed to carry out the first trials in the lake jointly. This means that from now on each farmer can operate individually. A basic goal of the spat-collecting function of Lake Grevelingen is also to make imports of foreign seed oysters unnecessary, thus minimising the risk of introduction of new diseases like *Bonamia*. A last, and important aspect is also that centuries of imports of seed oysters from southern, warmer countries like France and the Mediterranean had caused the native Dutch oysters to lose their original winter-hardiness. The oysters which had started the population in Lake Grevelingen had undergone a selection during the cold winter of 1962–1963 and appeared to have regained the original winter-hardiness of the native Dutch oyster. This is able to endure temperatures as low as the freezing point of sea-water without mortality, while imported southern oysters must be harvested before winter and must be stored in basins with heated water during frost spells. The water authorities still clung to the original plans that Lake Grevelingen should be converted into a fresh water lake as soon as the adjacent sea arm should contain fresh. This point of view was also defended by representatives from agriculture organisations, who considered it as a promise that they should get fresh water for irrigation. The good water quality and rich flora and fauna in the lake and its important role for the Dutch oyster industry, however, made that the original plans were reconsidered. Not earlier than in 1986 the decision was made to conserve Lake Grevelingen as a salt water lake. An ideal salinity in the lake was, in the meantime, safeguarded by the construction of a sluice and a siphon in the opposite closure dikes, making flushing of the lake with sea water possible. As said, these developments and management decisions have been of vital importance for our oyster industry. They can be considered to have saved not only the Dutch share in the European market of flat oysters, but they have also made possible the conservation of the native Dutch flat oyster as a genetic strain, which would otherwise have been lost.

6. CONSEQUENCES FOR FISHERY AND AQUACULTURE, RESEARCH AND THE RESULTING PROGNOSES

Despite all precautions, taken during the design of the Oosterschelde barrier and the secundary dams, the compromise between safety and nature conservation could not guarantee freedom from negative effects on nature and aquaculture. One of these was the risk of an increase of sedimentation on mussel rewatering plots off Yerseke, as a result of reduced current velocities. When this should happen, alternative occasions for mussel re-watering should have to be sought. Another question, very relevant to coastal as well as fisheries management, was whether the estuary would be capable in future to nourish as many organisms as it had done before. It was thought possible that the halved supply of nutrients would result in a decrease of primary production of phytoplankton and eventually in a shortage of food for filter feeders. Also the import of food particles from the North Sea could decrease. This could result in a reduction of the carrying capacity of the estuary. This question was imminent because the mussel cultivating industry was putting pressure on government to rent more plots to them, while number one priority in management of the estuary was the conservation of natural values. These interests could easily become conflicting when food supply in the estuary would be limiting for either the cultivated mussels or for wild organisms. Competition for food could then result in an undesired impoverishment of flora and fauna. Finally it was feared that the nursery function of the Oosterschelde for commercially valuable fish species would suffer from the reduced tidal volume. The amounts of planktonic fish larvae, carried in with the flood current could, it was feared, decline. The intertidal nursery area would be reduced by 20–30% by the decrease of the tidal amplitude.

Research

Negative impact on fishery and aquaculture except for the, already indemnified, oyster industry, could entail claims for damages brought out by the industry to the Government. An extensive research program was set up, first to study the original situation (which actually did not longer exist), second to make a prognosis for the changes to come. As far as the natural environment was concerned, these studies were carried out by the Ministry of Public Works and Waterways, responsible for the Delta Plan. Research in the field of fisheries and aquaculture was carried out by or in close cooperation with our institute.

Mussel Rewatering

The first priority for the management was a prognosis of the future sedimentation rate on the rewatering plots for mussels. Such a kind of research requires numerous sampling campaigns during an entire tidal cycle with up to six ships simultaneously. Thousands of water samples have to be analyzed in the laboratory and a multiple of this number of data, has to be processed. By combining the results of current and flow measurements and data about concentrations of suspended matter in the water with data about the accumulation of silt on beds of mussels, we arrived to the conclusion that the current velocities, expected to prevail on the rewatering location would just be sufficient to prevent accumulation of silt on the plots. This was much to the relief of the mussel traders, who exploit these plots, because otherwise they would have had to look for other locations. That the tolerable limit of the current velocity was almost reached appeared, however, in 1986 when the gates of the barrier had to be closed partially to ease construction works. During that period serious siltation occurred, inflicting damage to the mussel traders. Large amounts of silt had to be washed from between the mussels, mortality took place and the quality of the mussels was affected. Now the works have been finished and the definitive tidal regime is prevailing, siltation and mortality have ceased.

Carrying Capacity

The carrying capacity of the estuary for both wild and cultivated stocks of filter-feeding organisms appeared to be a very complex matter to investigate. We have, in first instance, limited our efforts to the availability of food for suspension feeders, notably mussels and cockles, (*Cerastoderma edule* L), as these groups are by far dominant in biomass and essential as food for migrating and wintering birds. This meant in the first place that an assessment had to be made of the biomass of these organisms and that their rate of food consumption had to be established. On the other hand, we wanted to know the quantity of available food in the water and its expected changes after completion of the Storm Surge Barrier. The first and most basic question, however, was: What is the food of filter feeders, what is its composition and what is the nutritive value of its components? It was discovered that particulate organic matter (POM) could be subdivided into a fraction which could be readily digested (70% or less) and a very stable one (30% or more). Also is was discovered that bacteria and small flagellates, although important in numbers, only had a very limited share in the cell volume biomass of potential food for filter feeders (Smaal c.s., 1986). Phytoplankton can constitute up to 20% (in weight) of POM in summer. An important food component for the filter feeders in the mouth of the estuary appeared to be relatively large phytoplankton organisms, imported from the North Sea by the tidal currents. This extra ration could be held partly responsible for the fact that the growth rate of mussels and cockles is high in the mouth of the estuary and declines along its length axis in upstream direction. (Van Stralen, 1988) Also it is felt, although not demonstrated, that this growth rate gradient finds its origin in food depletion, due to grazing by the filter feeders in the estuary. Research to elucidate this problem is still in progress.

7. EFFECTS OF CURRENT SPEED REDUCTION

The Lower Limit

More than any other form of mollusc cultivation, bottom culture is dependent on the tidal currents. The velocity of the currents above a culture plot leaves a certain tolerable range, within which bottom culture is possible. In mussel cultivation in the Oosterschelde, the lower limit for bottom culture is set by the total consumption of oxygen on and above the bottom on the cultivation plot. Four major oxygen consumers are active on a mussel plot: In the first place the mussels, second all other benthic organisms, in the third place the aerobic heterotrophic bacteria in the upper layers of the sediment and in the "benthic boundary layer". Another modest but important consumer of oxygen is hydrogen sulphide, produced by sulphate-reducing bacteria in the sediment. This highly toxic product diffuses up to the sediment surface and is normally oxydized in the top centimeters of the sediment. In sandy, well oxygenated bottoms, oxygen penetrates quite deeply, while hydrogen sulphide stays down. If, however, the sediment is muddy, the current velocity low and consequently the top layer of the sediment poorly aerated, hydrogen sulphide lingers just below the bottom surface and can reach the water phase and the mussels as soon as oxygen level is too low. In that case mortality can occur, not by anoxia, as is often thought, but by hydrogen sulphide poisoning. This can happen when current velocities are low and when the concentration of decomposing, oxygen-consuming organic matter in the water of the "benthic boundary layer" is higher than normal. In the Oosterschelde this has occurred when an algal bloom had died off and decomposed. A critical lower limit for current velocity is hard to give. When the organic matter content of bottom and water are low and the biomass of cultivated shellfish is not too high, e.g. lower than 3–5 kg fresh weight on a square meter, a current speed of some cm/s, or even a temporary current standstill around slack tide can easily be sustained. Such conditions are, to our experience, not favourable for a good mussel production but can be tolerated for instance on plots with small mussels. In contrast with the slow growth of adult mussels in Lake Grevelingen, where current speed ranges between nil and 20 cm/s, growth rate as well as meat yield of the native oyster *O. edulis* reaches high values. Apparently *O. edulis* is doing much better under low current conditions.

The Upper Limit

The upper limit of the sustainable current velocity range is set by purely mechanical and perhaps by trophic factors: Molluscs living on the substrate, like mussels or oysters, can lose their footing when current and/or waves exert an excessive stress on them. Also filter-feeding becomes less efficient at high current speeds, which mostly are linked to a high silt or sand load of the water. Also molluscs can be buried under shifting sediment, when current speed is very high. This burying can cause immediate death through suffocation, but also growth can be impaired due to loss of energy, when the animals have to clear their gills or have to dig out too frequently. We have tried to establish these upper current speed limits by measuring current velocities during two months on a number of locations: where mussel culture is profitable, where it is marginal and where it is impossible due to excessive current velocities. The results of this comparison are given in figure 5, which shows how frequently a certain current velocity is exceeded on a particular location. Mussel culture appears to be marginally possible on plots where a current velocity of 60 cm/s, measured 40 cm above the bottom, is exceeded during 5% of the time or more during an average tide. We consider this as the critical value, above which mussel culture is too risky to be commercially feasible (Steyaert, 1986). Most profitable mussel culture can generally be expected at current velocities in the range of 50–60 cm/s. Bottom composition is also an important factor for the grip mussels can have on their substrate. Older cultivation grounds, containing a fair amount of shell debris and a certain fraction of mud, appear to offer a better foothold for mussels than new plots with pure and mobile sand. Often, a period of initiation is required before new plots in high current areas become reliable.

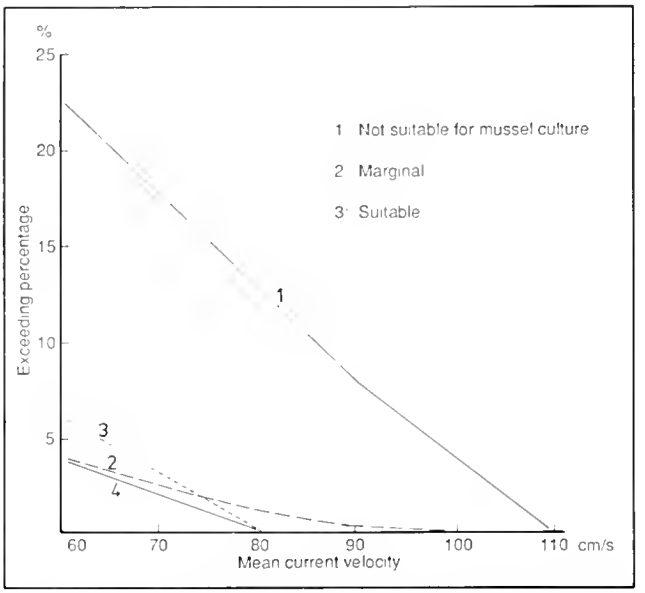

Figure 5. Exceeding percentages of maximal tidal current velocities on cultivation plots with different suitability for mussel culture. On the suitable grounds a speed of 80 cm/s is exceeded in about 4% of the cases. A reliable culture is only possible at speeds lower than 60 cm/s (Steyaert, 1986).

8. FISHERY AND AQUACULTURE IN THE OOSTERSCHELDE IN THE FINAL SITUATION

The construction engineers of the Delta project managed to keep their schedule better than the environmental researchers who had to make the prognoses for nature,

fishery and aquaculture: On the twenty-ninth of April 1987, the second of the two secondary dams was closed, which meant that the final shape of the Delta works was reached. Apart from some adaptation of the morphology of the estuary to the new hydraulic conditions, which may take more than 10 years, tidal movement and currents reached their definitive pattern. Already in the course of the works, it became clear that many of the design calculations for the Storm Surge Barrier had been carried out with a certain safety margin in favour of a larger aperture. Final measurements after completion of the works demonstrated that the volume of water flowing through the barrier each tide was larger than had been anticipated. This resulted in a mean tidal range of 3.20 m off Yerseke, instead of the 2.70 m originally deemed acceptable for the conservation of the environment. As the original tidal range had been 3.50 m, the final reduction of the tide appeared minimal: less than 10%. No wonder that mussel growers reported that they could hardly see any difference with the original situation on most of the cultivation plots. Only in one of the three tidal channels through the barrier, current velocities stayed below the original values. In two consecutive years, in the month of May, growth reduction and even mortality occurred on certain plots and the mussel growers complained. We assume the cause of this phenomenon to be the combination of a local decrease of the current speed with increased levels of organic matter in the water just after the yearly returning bloom of the flagellate *Phaeocystis pouchettii* in May. Probably oxygen depletion by the decomposing organic matter has caused anoxia and intoxication by hydrogen sulphide. This was confirmed by the presence of black, smelling mud. The mortality must have been increased by the usual post-spawning mortality of the mussels in that month. Further research will have to show whether this effect is lasting or not. Among the existing cultivation plots on the map of the Oosterschelde, covering some 3,000 ha, more than 30% are not utilized. After the start of the project, the succesive closing of the sea-arms caused a gradual increase of the sea-level and the current velocities in the area. This caused that a number of mussel plots had to be abandoned because either the mussels were swept away, or suffocated in "living sand". This caused that their productivity passed the limit of economic viability. The expected decrease of current velocities on a number of locations revived the interest of both fishery inspectors and mussel farmers in a number of plots which had been abandoned in the past decades. Site selection for bottom cultivation has hitherto been done by rather primitive means, based on the experience and intuition of professionals. No exact approach existed of the question whether or not a certain area is suitable for mussel cultivation. We, scientists think to have other means at our disposal for predicting possibilities for mussel cultivation that probing in the bottom with a boat-hook or spitting into the water to tell the current velocity. Although we may not dispose of generations of practical experience and green fingers, we have gathered the results of many months of continuous current measurements, and are able to fit these together and to make a mathematical model which can predict the current speed on any moment and on any location in the Oosterschelde at intervals of 100 m. The model outcomes were combined with the results of measurements with "Flachsee" type current meters on a selection of plots where mussel culture was profitable, just profitable or marginal. It appeared that at maximum flood current speeds higher than 60 cm/s at mid-depth no feasible mussel culture is possible, whereas in the range between 50 cm/s and 60 cm/s the risk for the mussels to be swept away is acceptable. (Van Stralen, 1988). At lower speeds mussel culture is possible, but too low current speeds entail, as has been exposed before, other risks. This operation yielded a set of current-charts on which the areas could be indicated where the current speed limit of 60 cm/s or of 50 cm/s at mid-depth will be exceeded during an average tide. The area where 60 cm/s will be exceeded will decrease considerably, whereas the area between 50 cm/s and 60 cm/s is expected to increase in comparison with the original situation. This is represented in figure 6 for an important mussel growing area, framed out in figure 3.

B. ASPECTS OF FISHERY AND AQUACULTURE MANAGEMENT

Fishery and aquaculture management in the Netherlands, carried out by the Ministry of Agriculture and Fisheries, has been confronted with various problems since the beginning of the Delta Plan. In the first place there was the problem of indemnification of the oyster industry. As we have seen, ten out of one hundred firms continued oyster farming. As soon as in 1976 it had become clear that the Oosterschelde would stay open, a number of other professionals, often the sons of former oyster growers, expressed the wish to re-start oyster farming and claimed a number of the cultivating plots which now were leased by the ten firms mentioned before. These, understandably, refused to give them back. This affair caused bitter discontent, resulting in the existence, now, of three separate associations of oyster growers and exporters. Another strong winter, followed by the outbreak of the oyster disease *Bonamia ostreae* postponed the solution of this problem. Instead, the battlefield moved to Lake Grevelingen, where, in 1977, the ten oyster firms had started their spat collecting project, had started growing marketable oysters, as well as a fishery for wild oysters. The success of this project did not stay unnoticed for long. In the first place there were the former mussel and oyster growers of the estuary. A number of the growers had opted for compensating plots in the Waddenzee, others had been granted eel fishing rights in Lake Grevelingen. These eel fishermen saw their former colleagues, even from a competing fishing-village, harvesting oysters in the lake where they were only allowed to fish

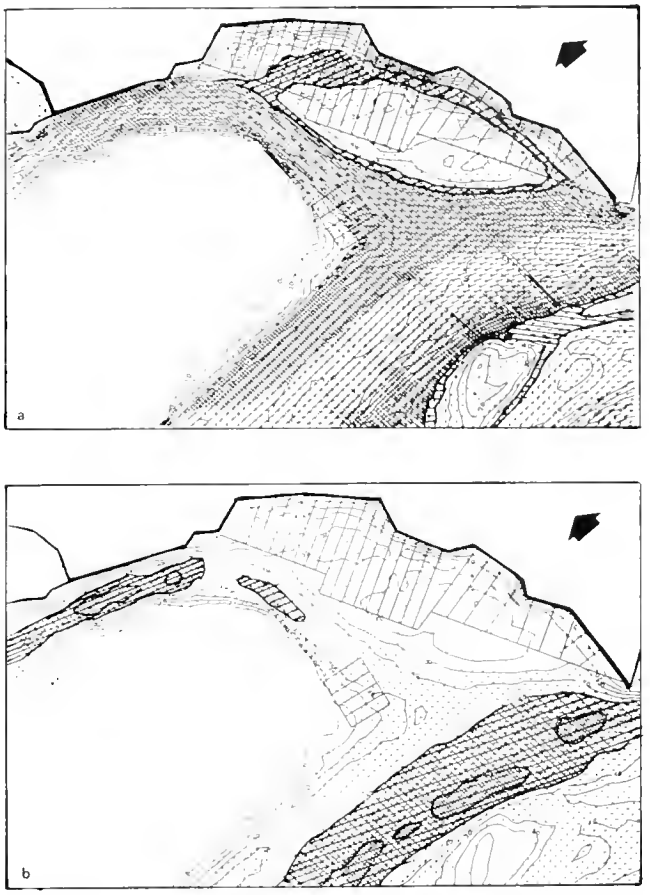

Figure 6. Current charts of the section of the Oosterschelde, framed in figure 3. The lined areas are plots for mussel culture. Fig. 6-a shows the original situation, fig. 6-b the situation after completion of the dams. The finely hatched area (in 6-a not filled) has current speeds over 60 cm/s, the coarsely hatched area has velocities between 50 and 60 cm/s. In the remainder of the channels in fig. 6-b current speeds are less than 50 cm/s. Scale 1: 50,000 (Van Stralen, 1988).

eels. They wanted their share of the newly discovered bounties of what they considered "their" fishing grounds. They argued that their catches did not meet the expectations and that they also wanted to lease concessions for spat collecting and oyster growing. The oyster farmers did not wish to allow anyone to participate in their project and, again, bitter quarrels followed. Both parties hired lawyers, who further sharpened the argument. The affair was made even more complicated because Lake Grevelingen was officially considered an inland lake. As never before oysters had been cultivated in an inland lake, the Inland Fishery Board, responsible for the issuing of fishing rights, now faced a problem it was not at all familiar with. Finally, it managed to untangle the Gordian knot and the compromise was found that the eel fishermen could rent a number of plots, on condition that they should sell their entire crop to the oyster farmers. In 1985, the Ministry considered the experimental project to be concluded and drew up a plan in which the culture area in the lake was to be increased gradually to 500 ha, and plots were issued to all practising oyster farmers. This meant that in total about fifteen firms could start producing oysters in the lake. In contrast with the first project, which had been carried out on a collective basis, individual firms had to lease plots. Again the established firms, this time in close harmony with the eel fishermen, opposed with all possible means the admission of other firms. Only in 1987 the judge ordered allotment of plots to all fifteen oyster firms. Since the start of the Delta Project, some hundreds of hectares of mussel cultivation plots in Lake Veere, in Lake Grevelingen and in the Oosterschelde had disappeared (figure 2). For most of them compensating culture ground was found, mostly in the Waddenzee, where now an area of about 6,000 ha is in lease. A further extension of the mussel cultivating area in the Waddenzee is restricted by the shrimp fishing industry in that area. Unfortunately both the shrimp fishermen and mussel growers prefer the same areas. The shrimp fishermen already saw an increasing portion of their fishing grounds occupied by mussel plots, on which they are not allowed to fish with their trawlnets. At this moment, all suitable grounds are occupied and there is little scope for amplification of the mussel growing area. Another factor is that nature conservationists are looking to mussel culture with more critical eyes than before. Possible depletion of food for other filter feeding organisms by the mussels on the cultivation plots and the fear for alterations of the natural environment around mussel plots, has made nature conservation authorities first want to know if the mussel growing has a negative impact on the environment before any new concessions are allowed. As has been exposed above, the reduction of the current velocities in the Oosterschelde is expected to make mussel culture possible on a number of places where before current velocities had prevented this. Whether or not this potential cultivating ground will actually be destined for the mussel growing industry will mainly depend on the outcome of the investigations into the carrying capacity of the Oosterschelde. Management of shellfish cultivation and fisheries is, in these days, not longer a matter of the fishery authorities alone. Following a modern trend, in the Netherlands on this moment three ministries are responsible for environmental management. As bottom culture of mussels is often carried out in areas of outstanding natural interest, all human activities in these areas, even if they look as environment-friendly as mussel cultivation, are watched with a critical eye. It seems that at last this industry, which has been able to proceed and to flourish practically undisturbed since its birth in 1870, will finally be subjected to the restrictions and regulations of modern society.

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NEW JERSEY'S COASTAL WATER QUALITY MANAGEMENT PROJECT—METHODOLOGIES FOR THE PROTECTION OF ESTUARINE WATER QUALITY AND SHELLFISH RESOURCES

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ABSTRACT Degradation of estuarine water quality is the result of increased residential and commercial development throughout New Jersey's coastal region. Nonpoint sources and stormwater runoff are the primary pollutant sources from this development, as point sources have generally been eliminated. This has resulted in the restriction of important water uses, such as shellfish harvesting and primary contact recreation, in waterways that were formally of great value. New Jersey's Department of Environmental Protection realized that existing water quality management programs were not adequate from the standpoint of controlling runoff and other nonpoint sources. The Department has developed a water quality and shellfish resource assessment methodology that defines past and current conditions of specific estuarine waterways. The results are used to determine the degree and type of water quality management actions necessary for the protection of water quality and designated uses. Management programs are coordinated through State, county and municipal planning activities. The assessment methodology can be applied to a variety of water uses and waterbody types.

KEY WORDS: Water quality planning, shellfish resource assessment

INTRODUCTION

New Jersey's coastal waters have served as an important source of the nation's shellfish during the past century. Commercially, the hard clam (*Mercenaria mercenaria*), soft-shelled clam (*Mya arenaria*), eastern oyster (*Crassostrea virginica*), blue mussel (*Mytilus edulis*) and surf clam (*Spisula solidissima*) are taken from the State's waters. In 1984 the commercial landings of shellfish in New Jersey had a dockside value of over $46 million (Robinson, 1986). In 1985 approximately 28,000 hard and soft clam recreational licences were issued by the State, indicating that shellfish also support an important recreation activity. The NJ Department of Environmental Protection (NJDEP) (1984) estimated that over 2.7 million people annually participate in marine sport fishing and shellfishing. Although the State's shellfish industry is not as prominent as it was earlier in this century, it remains a significant local industry.

The past two to three decades have witnessed extensive residential and commercial growth in the four coastal counties of the State. While the State's population grew 3 percent between 1970 and 1980, the four coastal counties had an average growth of 31 percent. Projections indicate population will grow an additional 38 percent to the year 2000 for the four coastal counties (NJDEP 1985). This would place approximately 1.5 million residents within a few miles of the coast.

Water quality conditions in the bays and estuaries of the coast have deteriorated as a result of the increasing population and development. This deterioration has continued, although somewhat abated, even with the recent elimination of many antiquated or improperly operating sewage treatment facilities that were discharging to bays or tidal streams. While a reduction of condemned shellfish harvesting waters did occur with the move to larger, more efficient regional municipal sewage treatment systems that discharge to ocean waters, the anticipated improvements in estuarine water quality have not been fully realized. This has led State water quality and shellfish classification agencies to suspect nonpoint sources of pollution to be a much greater source of pollution than originally thought. In fact, recent studies by the NJDEP show that nonpoint sources of pollution are degrading water quality in the State, and that their effects are especially pronounced in estuaries and bays (NJDEP 1982 and 1987; Connell and Vernam 1987; and Robinson 1986).

Monitoring of estuarine and ocean waters adjacent to bathing beaches found that total and fecal coliform readings were highest in bay waters and after rainfall events (NJDEP 1987). In the Navesink River estuary, Monmouth County, urban runoff and agricultural runoff via tributaries were identified as the cause of closed and restricted shellfish growing waters (NJDEP 1982). Connell and Vernam (1986) compared pollutant levels at a marina in an open-ended waterway with unrestricted flow to levels near a marina in a closed-ended channel. The close-ended channel with restricted flow and poor flushing ability had higher coliform levels and oxygen-demand in the water column, and petroleum hydrocarbons in sediments. Elevated pollutant levels also appeared to be associated with greater human and boat activity.

The rapid residential and commercial growth in the coastal area of the State threatens to further degrade the quality of waters which currently support, or have the potential to support, various water-based uses. Therefore, the NJDEP initiated the Coastal Water Quality Management Project (CWQMP) to manage pollution sources affecting estuarine waters. The project attempts to coordinate water

pollution control activities with important resource and water-use goals. The CWQMP is a cooperative planning effort involving the NJDEP's Division of Water Resources, Division of Coastal Resources, and Division of Fish, Game and Wildlife. Protection of shellfish resources and the in-stream water quality needs for harvesting the resource are the initial priorities of the project. The CWQMP has been designed to summarize water quality and shellfish resource inventory information in the context of compliance with clean water goals of federal and state legislation; and to utilize existing, or develop new, programs for implementation of appropriate resource and water quality management actions. This paper summarizes the methods in the CWQMP and presents the initial results of the project's application to selected coastal waterways.

A SYNOPSIS OF COASTAL RESOURCE AND WATER QUALITY MANAGEMENT PROGRAMS IN NEW JERSEY

Responsibility for the protection and maintenance of coastal water quality and natural resources in New Jersey lies primarily at the state level in the NJDEP. Within the NJDEP, the Divisions of Water Resources, Coastal Resources, and Fish, Game and Wildlife are the principal agencies conducting programs for this purpose. Various federal and local agencies also conduct their own programs alone or in conjunction with State programs.

The Division of Water Resources (DWR) oversees a number of programs that control pollutant discharges to the State's waters. These programs are the result of both national and state clean water laws. Water quality management programs range from the setting of water quality standards and stream classifications, to monitoring, planning, state and national pollutant discharge permits (New Jersey Pollutant Discharge Elimination System permits), stormwater management regulations, and a variety of other regulatory or voluntary initiatives. The DWR also provides input into numerous other programs that deal directly or indirectly with the State's water resources.

The Division of Coastal Resources (DCR) was created to consolidate implementation of the Coastal Areas Facilities Review Act (CAFRA) of 1973, the Wetlands Act of 1970 and the Waterfront Development Law of 1914, for the purpose of ensuring the protection and proper use of the State's coastal areas. The Division's policies and regulations for coastal resource protection are defined in the *Rules on Coastal Resources and Development* (NJDEP 1986). CAFRA permits are required for all major residential (25 or more dwelling units), industrial, transportation, utility and energy-related facilities in the coastal area. In addition, Waterfront Development Permits are issued for all construction or development activities along the edge of navigable waters. These activities include bulkheads, docks, storm drains, etc. Wetlands permits are required to excavate, dredge, fill or erect structures in or on coastal waters. A variety of agencies within the NJDEP review CAFRA and Waterfront Development permits for consistency with their appropriate program objectives. The DWR often required specific stormwater management controls (primarily detention and retention basins) as part of these permits when stormwater is expected to have impacts on receiving water quality.

The Marine Fisheries Administration, Division of Fish, Game and Wildlife (DFGW), has responsibility for marine fisheries resource and habitat conservation, and for ensuring the continued productivity of New Jersey's marine fin and shellfisheries. Within the Marine Fisheries Administration, the Bureau of Shellfisheries issues commercial and recreational clamming licenses, defines the size and number of lease lots for commercial harvesting or relaying, and conducts resource studies. The DFGW also reviews CAFRA, Waterfront Development and DWR-issued permits to ensure that marine fisheries resources will not be adversely impacted by the proposed actions.

Despite the presence of these agencies and programs, the quality of many coastal waterways have declined over the past few years. It is apparent that existing programs of water quality management in the State are not fully adequate for the protection and restoration of water quality in the coastal region. Increased emphasis on the control of pollution from nonpoint sources and stormwater runoff is necessary.

DESCRIPTION OF THE COASTAL WATER QUALITY MANAGEMENT PROJECT

The CWQMP was devised in early 1986 after a series of meetings were held between representatives of the NJ Divisions of Water Resources, Coastal Resources, and Fish, Game and Wildlife for the purpose of exploring ways to protect water quality and shellfisheries of coastal bays and estuaries from increasing pollution due to development. Because of inadequate water quality and resource management strategies for individual coastal waters, programs in the State were not strong enough to support denial of permit applications or require appropriate permit conditions for developments near important shellfish growing waters. Many of these developments would undoubtably have water quality impacts from nonpoint sources and stormwater discharges. Therefore, a primary goal of this working group was to collect all available information on water quality and shellfisheries resources for each coastal waterway so that detailed assessments could be made. The assessment would then lead to specific water quality and shellfish resource management objectives for the particular waterway, as well as provide the basis for making sound regulatory decisions.

The general framework for the CWQMP is based on a study by the Virginia Interagency Task Force on Shellfish Resources (1982). This study recommended that the state's shellfishing growing areas be evaluated with a water quality and biological index. New Jersey's CWQMP takes a similar approach. The CWQMP's working group devel-

oped a rating system that would assess water quality conditions, pollution sources, shellfish populations and recreational/commercial uses of the shellfish. The rating would be applied to individual or grouped waterways, or sections thereof, in a manner consistent with present shellfish water classification sanitary survey area boundaries. All available information of value in rating the waterways would be collected in detailed segment descriptions. The State's bays and estuaries are separated into approximately 30 segments, each will undergo the assessment and rating procedure.

The rating system has two sections: a water quality assessment and a shellfish resource assessment. Both assessments have a rating scale from 0 to 100. For water quality, a lower rating indicates better water quality and few pollution sources. A low shellfish resource rating represents low resource density and little commercial/recreational value. Figure 1 indicates qualitatively what the water quality and shellfish resource ratings signify.

TABLE 1.

Summary of the Water Quality Assessment Rating

1. Classification of Segment (percentage of area) × Rating Value	
Classifications:	Rating:
Condemned without use	50
Condemned with use	40
Special restricted	30
Seasonal	10
Approved	0
2. Pollution Sources—Each rated on a scale of 0 (no impact to water quality) to 10 (severe impact). Maximum 50 points for pollution sources.	
Sources:	
Point sources	
Nonpoint sources	
Boatslips	
Marinas	
Tributary inputs	

Water Quality Assessment

The assessment procedure for rating water quality includes a review of current water quality conditions, and the types and extent of pollution sources (Table 1). This review is primarily based on the results of sanitary surveys. The status of water quality in a segment is represented by the shellfish harvesting classification(s) assigned to the waterways, and as such, is a summation of bacterial concentrations in the water. These classifications include: approved for harvesting, seasonally approved, special restricted (harvesting allowed but further cleansing of the shellfish required), condemned with use (shellfish allowed to be transplanted), and condemned without use. The criteria utilized by the NJDEP for classifying shellfish growing waters are described by the US Department of Health and Human Services (1986). The percentage of an area's classifications, as a percentage of the total area, is multiplied by a rating value. Each rating value is specific to the type of classification. The rating values and corresponding classifications are presented in Table 1. The classification chart rating can range from 0 to 50 points; higher points indicate more restrictive classifications and poorer water quality.

The second section of the water quality assessment consists of a rating of known and potential pollution sources. The five rated sources include point sources, nonpoint sources, boat slips (docks), marinas and tributary inputs. Each source is measured on a scale from 0 to 10, with 0 representing no impact and 10 significant impact. The pollution source section can receive a possible maximum of 50 points if each of the possible sources rates the maximum of 10. Point sources are defined as permitted wastewater discharges. The number of stormwater runoff discharges is the primary determination for nonpoint source impacts. Boat slips and marinas, often a source of bacteria pollution in estuaries, are considered separately because their water quality impacts can be locally significant. The purpose of including tributary impacts is to review the general extent of pollution entering the segment from freshwater tributaries.

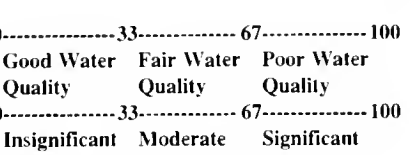


Figure 1. Interpretation of Rating Values

A Detailed Segment Description (DSD) is produced to support the water quality assessment rating. This description is designed to collect and summarize all information necessary to accurately characterize water quality conditions and pollution sources. In the DSD water quality conditions and trends are determined by the following:

—Classification chart review (changes in classifications for the past 10 years);

—Summary of coliform data collected for sanitary surveys for the past 10 years;

—Summary of data collected for summer bathing beach surveys for 1985 and 1986; and

—Summary of water quality data collected from freshwater tributaries for the past 10 years.

Known and suspected pollution sources in a segment are reviewed from the following information:

—Presence and location of permitted point source discharges;

—Location and number, by municipality, of stormwater discharge pipes;

—Inventory of marinas, including data on marina size (number of slips), boat size permitted, and the availability

of toilets, showers, pump stations and fueling operations; and

—Population and growth statistics for surrounding communities, including building permits, as a general indicator of potential nonpoint sources.

The water quality assessment and rating is conducted by the agency in the State responsible for classifying shellfish harvesting areas (Bureau of Marine Water Classification and Analysis, NJDEP). Much of the water quality and pollution source information is mapped on a series of overlays. The overlays provide a quick visual representation and often show simple cause and effect relationships between water quality and the pollution sources in the segment.

Shellfish Resource Assessment

The shellfish resource assessment provides a rating of the shellfish resources found in a particular segment (Table 2). In addition, it rates the recreational and commercial uses that may be occurring. As with the water quality assessment, a DSD on the shellfish resources is compiled as a back-up information source to the rating. The Primary Shellfish Population Density Rating section rates the percent density of an area by the major shellfish population. The rating is on a scale from 0 to 75, and has three categories: occurrence, moderate density and high density. An occurrence has a shellfish density of 0 to 2.0 shellfish per square meter, a moderate density is 2.1 to 5.3 shellfish per square meter, and high density is 5.4 shellfish or greater per square meter. An occurrence receives a rating of 25, while a moderate density is rated 50, and a high density 75. The density rating is then multiplied by the percent coverage of the area. This rating applies only to the primary shellfish species present in the segment. To account for other species present, supplemental values are given for shellfish of secondary importance. The presence of a secondary species can add three points for presence and 10 for the occurrence of beds. Valuable habitat characteristics, the presence of eel grass (*Zostera marina*) can also add 10 points to the rating. Together, the density rating and supplemental value can be a maximum of 75 points.

The second part of the shellfish resource assessment rates the use of the shellfish in the segment. A total of 25 points are possible in this section, 15 for recreational value and 10 for commercial value. Additional commercial value points are given for depuration (5 points), relay harvesting (5 points), relay planting (10 points), and the presence of leases (10 points).

Shellfish resources and use are explained specifically in the DSD. Historical and current information on the location and density of all shellfish species found are described. A 1963 survey of the State's shellfisheries provides the historical sketch, while an on-going shellfish inventory is the basis for the current information. The combination of past and present data on the shellfish resource can assist in determining natural production potential and the possible affects on the resource by human activities, such as overharvesting, channel dredging, and development.

As with the water quality information, much of the shellfish resource data is mapped on a series of overlays. The presence of shellfish resources as related to current water quality conditions and pollution sources can be identified. The shellfish resource assessment ratings are completed by the Bureau of Shellfisheries, DFGW.

TABLE 2.

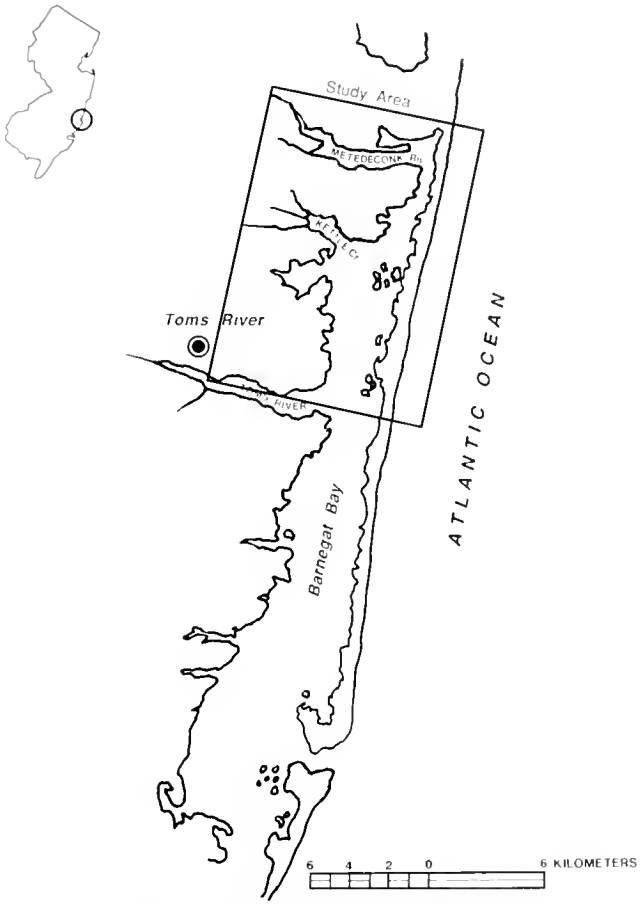
Summary of the Shellfish Resource Assessment Rating

1. Primary Shellfish Population Density Rating (maximum of 75 points)	
a. Percent density of area by the important shellfish population.	
Density:	Rating:
Occurrence	25
Moderate	50
High	75
b. Supplemental ratings for populations of secondary importance and the presence of valuable habitat.	
1. Presence of population (3 points)	
2. Occurrence of beds (10 points)	
3. Presence of eel grass (10 points)	
2. Uses of the Shellfish Resources (Maximum of 25 points)	
a. Recreational (0–15 points)	
b. Commercial (0–25 points)	
1. Use	10 points
2. Depuration	5 points
3. Relay Harvesting	5 points
4. Relay Planting	10 points
5. Leases	10 points

APPLICATION OF THE CWQMP

The CWQMP has been fully applied to two back-bay areas along the Atlantic Coast, Upper Barnegat Bay and Atlantic County back-bays north of Atlantic City (Figures 2 and 3). Both areas are experiencing significant residential and commercial growth, raising concerns over the impacts on water quality from stormwater discharges and nonpoint sources of pollution. Both waters include important shellfish resources or management uses. The two areas have been rated for water quality and shellfish resources, and have complete DSDs.

1. Upper Barnegat Bay—The Upper Barnegat Bay segment encompasses two santitary survey areas that total 4197 ha in size. Upper Barnegat Bay, originally a closed-ended waterway, is now flushed via a canal to the north and an inlet approximately 22 km to the south. Upper Barnegat Bay was rated as having moderate water quality (rating of 57), based on harvesting classifications and pollution sources. Nonpoint sources, marinas, docks and tributary inputs were all considered to have significant impacts on water quality. The classification chart and pollution source ratings averaged 29 and 28, respectively. Much of the segment is closed or restricted at times in the year for shellfish harvesting, although some areas remain open year-round. An overall trend of declining water quality in the segment



Location of the Upper Barnegat Bay study area.

is occurring as new development extends throughout the watershed region. Proposed reclassifications would downgrade nearly 120 ha of the segment.

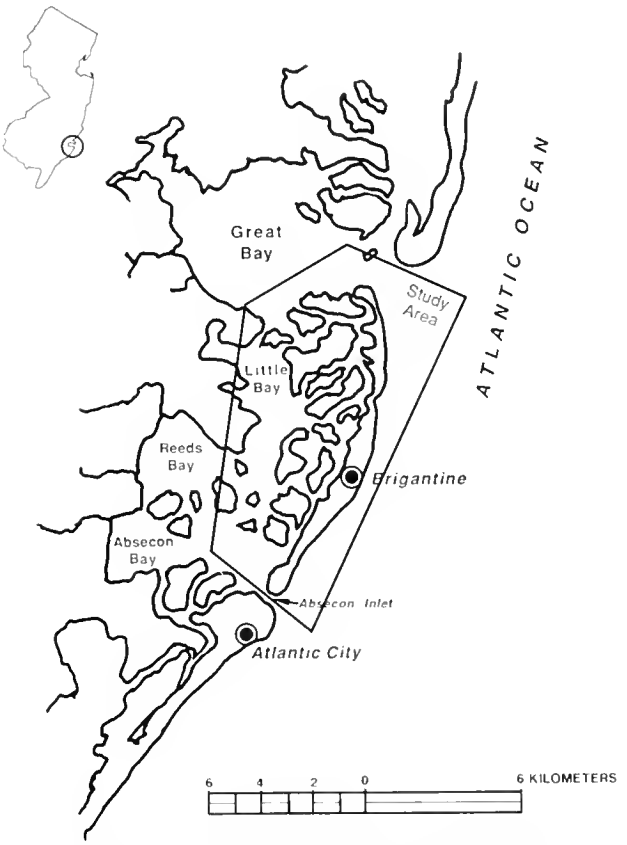
A moderate shellfish resource rating of 48 was obtained for the northern one-half of Upper Barnegat Bay, compared to a low resource rating of 15 for the southern one-half of the segment. Even though the entire segment contains low density resources there is a relay planting bed in the northern section of the segment. The relay bed is the northern-most relay point on the coast and is important for clammers who relay from productive special restrictive waters located to the north.

2. Atlantic County Back-bays North of Atlantic City—The second study area includes the back-bay waters of Atlantic County northwest of Atlantic City. The segment, consisting of approximately 1050 ha, includes a number of small bays, and a large amount of open and closed-ended channels. These waters are generally of good water quality, as demonstrated by the low water quality rating of 10 for the segment. Most of the area is open for shellfish harvesting. Only low to moderate amounts of pollution were attributed to stormwater discharges, boat slips and tributary inputs. Certain sections of this segment have experienced heavy growth during the past five years. As a result, stormwater and nonpoint source impacts are becoming significant locally.

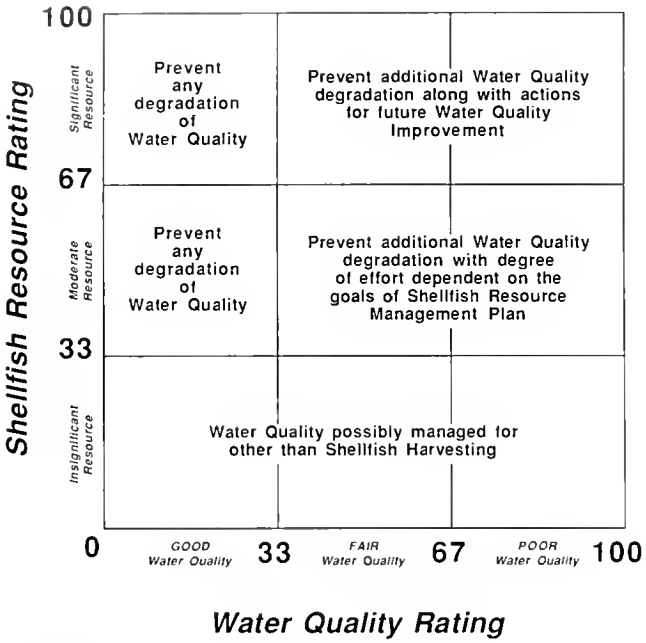
A high density hard clam resource is found throughout the segment, resulting in a high shellfish resource rating of 88. This rating is not based solely on the clam densities, but also on the recreational and commercial uses occurring (includes relay harvesting and leases). A recent resource survey of one waterway, St. Georges Thorofare, found a hard clam density among the highest reported in the Middle Atlantic states region (an average of 10.4 clams per square meter). Because current resource information was not available for much of the segment inventory data from 1963 was utilized for assessing the majority of the segment's resource density and occurrence.

THE NEXT STEP IN THE CWQMP—DEVELOPING MANAGEMENT GOALS AND PROGRAMS

The ultimate purpose of the CWQMP is to develop and implement activities for the better management of coastal water quality and the region's valuable water-based resources/uses. Figure 4 presents the conceptual water quality and shellfish resource management strategies which would be assigned to waterways based on the assessment procedure of the CWQMP. As such, water quality and resource management goals can be tailored to each waterway.



Location of the Atlantic County back-bays study area.



Conceptual management strategy for water quality and shellfish resources.

Various management options were identified during the initial application of the CWQMP that would be necessary in the near future because of the continued development of waterfront and near-coastal lands. For the purpose of this study these options can be grouped into two general categories: shellfish resource management and water quality management.

1. Shellfish Resource Management—New Jersey lacks a comprehensive shellfish resource management plan that would address specific management strategies by waterway for resource potential and use. The resource assessments prepared for the CWQMP could serve as the basis for the strategies in the comprehensive plan. Up-to-date resource inventories are only available for one-half of the coast; these inventories must be completed for the remaining waters and a system for periodic revisions implemented. The resource management strategies would also be related to the water quality goals identified for each waterway.

2. Water Quality Management—The control of nonpoint sources and stormwater discharges entering coastal waters was an initial reason for developing the CWQMP. Subsequently, water quality management activities will focus on identifying and managing these pollution sources. State, county and local water pollution control planning will be proposed to identify specific nonpoint sources, stormwater discharges and other pollution sources affecting water quality as part of a water pollution control plan for the particular locality. State water quality management planning regulations will require such planning. Control and implementation strategies would also be a requirement. Planning activities would determine the water quality goals for each waterway. In the future, discharge permits will likely be required for stormwater drainage systems discharging significant amounts of pollution. Control of pollution from upstream areas via tributaries, and from boating/marina facilities will also be necessary in many waters.

CONCLUSIONS

The environmental and economic reasons for the CWQMP are clear. But the CWQMP is also attempting to develop a framework for consistent, clear and effective decision-making so that New Jersey can successfully manage the water quality needs of the State's coastal waters. This is especially critical with regard to the proper management of nonpoint sources and stormwater quality. Preparing a thorough inventory and management plan for the State's shellfisheries resources is equally important. The CWQMP is a critical and initial step towards these goals.

The project's methodology also provides a structured and defensible approach for regulatory processes. Decisions regarding the approval or denial of permit applications can be made more rapidly and in a manner consistent with the water quality and resource goals of a waterway.

The results from the initial application of the CWQMP appear consistent with the intended goals of the project. The ratings reflect the variations in water quality and shellfish resources between the two areas. The accompanying Detailed Segment Descriptions include all the pertinent and available information that can be reasonable gathered with which to characterize water quality, pollution sources, and shellfish presence and value. In addition, all the data utilized in the project was already existing, thereby not requiring any time consuming field work. The summarized data assists in clarifying conditions in the segment so that decisions regarding water quality management or shellfish resource protection can be consistently made. Subsequent to the completion of the two study areas, rating assessments and DSDs have been nearly finished for the northern coastal county. Coast-wide application is expected.

Other uses of estuarine waters, such as the protection of swimming areas, will be assessed by a similar rating and information management system. Finally, New Jersey's freshwater streams and lakes requiring both water quality and resource management actions are also expected to be rated in a fashion comparable to the CWQMP.

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PUBLIC HEALTH COMPONENT OF BIVALVE SHELLFISH PRODUCTION AND MARKETING

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ABSTRACT Public health provisions are an essential component in the chain of activities involved in production, harvesting, and marketing of bivalve shellfish for human consumption. Unfortunately, the public health component is often minimized, or completely overlooked, in the development and management of shellfish culture or harvesting activities. One aspect of shellfish sanitation that has received considerable attention and publicity in recent years is a form of wet storage often referred to as depuration. The efficacy and unility of depuration is contingent upon many variables such as, the species of bivalve, the type and concentration of the contaminant, and the social, economic, and technical constraints influencing plant operation. The nature of these limitations and their implications for the appropriate application of the process will be discussed. An increasingly important aspect of shellfish sanitation, as pertains to products of aquaculture systems, is considered.

KEY WORDS: Shellfish sanitation, bivalves, public health

INTRODUCTION

Public health provisions are an essential component in the chain of activities involved in production, harvesting and marketing of bivalve shellfish for human consumption. Certain unique features of these provisions are a consequence of the capacity of filter feeders to concentrate and accumulate a variety of contaminants from the waters in which they grow.

Unfortunately, the public health component is often minimized, or completely overlooked, in the development and management of shellfish culture or harvesting activities. However, without an effective shellfish sanitation program that will assure a product having an acceptable health risk for the consumer, no system of shellfish production and marketing, regardless of the appropriateness and efficiency of its other components, is acceptable by current standards.

Basically, a shellfish sanitation program includes: an *infrastructure* (usually composed of public agencies) capable of assessing growing water quality (classification), monitoring culture and harvesting activities, and providing adequate surveillance of the chain of supply from the point of production to the point of retail (includes maintenance of product identity and testing market shellfish for contaminants); an *administrative system* for coordinating the activities of the various agencies responsible for executing the program, both within the producing areas and between the producing area and the receiving market areas; *appropriate legislation* empowering the responsible agencies to enjoin and prosecute violators of the program. The major features of a shellfish sanitation program will be amplified and discussed, pointing out the necessity of interaction of the industry members with the regulatory agencies in formulating and executing the program.

One aspect of shellfish sanitation that has received considerable attention and publicity in recent years is a form of wet storage often referred to as depuration. This process involves post-harvest maintenance of bivalves in tanks of seawater, under conditions that stimulate physiological activity, thus favoring unloading or elimination of contaminants by normal biological mechanisms of the shellfish. The efficacy and utility of depuration is contingent upon many variables such as the species of bivalve, the type and concentration of the contaminant, and the social, economic, and technical constraints influencing plant operation.

ACCUMULATION OF CONTAMINANTS

Many aquatic organisms gather their food by entrapping fine particles suspended in the water which surrounds them. In the case of bivalve molluscs the mechanism involved is conventionally described as filter feeding. Briefly, the mechanism is composed of a means of moving (pumping) relatively large volumes of water across and through a "filtering" surface (gills) upon which the particles are entrapped, sometimes with considerable selectivity, and from which they are then transported to the digestive tract of the animal.

The details of this mechanism need not be examined here; it is sufficient to note that the capacity of this system to remove particles, of a broad range of sizes, from a very large volume of water is highly developed in many species of bivalves of commercial importance (Galtsoff 1964; Bayne and Widdows 1978; Vahl 1972, 1973; Galassi and Canzonier 1977, Winter 1978). There is some evidence that this feeding mechanism may also be involved in the uptake of dissolved materials from the pumped water (Cunningham and Tripp 1973; Pringle et al. 1968; Pentreath 1973.)

The particles removed from the environment are concentrated to levels many times those found in the water; the concentration factor may be in the range of 10 to 1000 or

more. A certain fraction of the particles is accumulated in one or more "compartments" of the bivalve: the peribranchial chamber; the gill surface; the pseudofeces; the gut lumen; various tissue spaces; within cells adjacent to the gut lumen; and entrained in the exiting feces. Some of these captured particles are destined to be partially or completely degraded, thus making their components available to the nutritional pool of the bivalve. However, some particles may be at least partially refractory to degradation and capable of persisting unchanged within the animal. The duration of retention of these particles will be a function of the composition of the sequestered material as well as the particular compartment in which it comes to reside (Stauber 1950; Tripp 1960; Feng 1967; Feng & Feng 1977). For example, a bacterial cell confined to the gut lumen may be unloaded within a matter of hours after ingestion, whereas, a viral particle that has been phagocytized by a hemocyte or a fixed cell in the digestive gland may persist in recoverable form for a period of several months if its essential components are refractory to the digestive processes of the cell. Certain components, for example phytotoxins, may be selectively retained in some of the tissues.

It is due to this capacity of bivalves to concentrate and accumulate materials from the environment, coupled with the tradition of consuming shellfish raw or only lightly cooked, that bivalve molluscs present a rather unique risk for the unwary consumer. Among the materials that might be sequestered by feeding bivalves are several potential etiological agents of human diseases. The earliest recognized of these disease agents were the bacterial enteropathogens, e.g. the *Salmonellae* that cause typhoid (Bulstrode 1896; Herdman and Boyce 1899; DeGiaxa 1889). Much later, algal toxins from phytoplankton, heavy metals (mercury) and enteroviruses (Richards, 1985) were added to the list. Potentially, other chemical agents, both inorganic and organic, might be suspected as creating risks; however, epidemiological evidence has not indicated any significant problems in this area (Butler 1966, 1974; Portmann 1975; Neff and Anderson 1974; Morales-Alamo and Haven 1983; Stegeman and Teal 1973; Fossato and Canzonier 1976; Schulz-Baldes 1974, DiSalvo et al. 1975).

Clearly, due to the unique risk factor associated with the accumulation capacity of bivalves, the growing, harvesting and marketing of shellfish requires some rather special precautions in order to adequately protect the public health.

SHELLFISH SANITATION PROGRAM

The formal structure of the shellfish sanitation program in each state, or other political subdivision, is usually the responsibility of one or more governmental agencies (e.g. health, natural resources or environmental protection agencies). In the case of countries outside the USA or Canada, the program may be exclusively administered by a national agency. In many cases the actual operational components of the program may include municipal or county level agencies. For over a half century the programs in the individual producing states has functioned under a set of guidelines that are the product of the National Shellfish Sanitation Program. Coordination of this national program and the supervision and evaluation of the individual state programs is the responsibility of the U.S. Food and Drug Administration.

The establishment and promulgation of the set of guidelines, under which the individual state programs operate, is the result of a collaborative effort of the FDA, the representatives of the state agencies, committees of technical specialists and members of the shellfish producing and marketing industries. This collaborative effort is modeled on a similar system that regulates the production and marketing of dairy products. The guidelines are formulated, updated and promulgated on a continuing basis by the Interstate Shellfish Sanitation Conference (ISSC), and they are published in a Manual of Operations (ISSC 1987), which is available to all interested parties. The Manual spells out in detail how a program should be operated in the member state and the interrelation of member state programs; it cites the criteria to be applied by the FDA in evaluating the efficacy of the programs in each member state.

Since the sanitary quality of growing waters is of primary importance in the production of safe shellfish, there is considerable emphasis on the procedures to be used to characterize and classify the shellfish producing waters. As a complementary crosscheck it is required that the product be sampled and assayed at various stages from harvest through the chain of distribution up to the point of retail sale. Of considerable importance, and no easy task, is the maintenance and assurance of identity of origin of the product throughout the chain of distribution. The minimal agency infrastructure, the technical and administrative methods to be used in the field and laboratory and the standards of acceptable quality for the product and the minimum requirements for the physical facilities and operational practices of the commercial handlers are presented in detail, with accompanying rationale, in the Manual.

Operation of a shellfish sanitation program requires an appropriate administrative infrastructure that will assure adequate coordination of the numerous and varied field survey and product monitoring activities, laboratory operations and data processing and evaluation. In addition, effective and rapid intercommunication with, and records transfer to, all responsible authorities is essential to permit tempestuous intervention in situations that might have compromised the quality of the product released to the market as well as to demonstrate compliance with the mandates of the program at the time of periodic evaluation by the FDA.

Obviously, the responsible agencies must have sufficient statutory authority to carry out their various regulatory functions. These functions include the power to prevent production and harvesting of shellfish in unacceptable

growing areas, authority to monitor the harvesting, processing and distribution of shellfish, including sampling the product, and the power to sequester or prevent transfer of a shipment of shellfish when this is deemed necessary to protect the public health. Some of these functions may be shared with, or delegated to, specific law enforcement agencies within the state. Such powers must have a firm basis in the state statutes or administrative regulations. Strangely, this aspect is often overlooked in developing a shellfish sanitation program.

DECONTAMINATION OF SHELLFISH

As coastal populations increase in density there is an ever greater input of contaminants to shellfish growing waters with a consequent increased public health risk. This situation has resulted in further restrictions on the utilization of valuable shellfish resources. To compensate for the loss incurred by the application of shellfish sanitation growing water standards, several "corrective" measures have been repeatedly proposed. These measures are often intended to reduce the risk associated with the consumption of shellfish harvested from polluted waters, but do not address the basic problem: the input of contaminants to the growing waters.

One procedure that can often be successfully applied is adequate cooking, essentially sterilization, of the shellfish prior to marketing (e.g. cockles (*Cardium* spp.) in England; mussels (*Mytilus* spp.) and hen clams (*Venus gallina* L.) in the Mediterranean). Obviously, this solution is appropriate only for bivalves which contain heat labile microbial contaminants and which are acceptable by the consumer as a cooked product. Another effective intervention is the practice of relaying shellfish from polluted waters to approved areas for relatively long periods (30 days or more) to permit them to purge themselves of contaminants prior to harvesting for market. This practice is feasible only when the initial cost of collection is relatively low, the retail value of the species is high, the relayed stocks can be adequately monitored to prevent unauthorized harvesting, losses due to replanting and subsequent recovery are not excessive and the reharvest efficiency is high. In some situations this practice is utilized by conservation and sanitation agencies to deplete stocks in polluted waters in order to reduce the incentive for illegal harvesting; this is an added benefit which may render the practice cost effective.

An alternative procedure that may permit the utilization of shellfish from moderately polluted waters is the application of the process of depuration prior to marketing. This method, which might be thought of as a sophisticated variation of controlled relaying, has seen documented use in Europe for over seventy years (Johnstone 1914, Dodgeson 1928). Briefly, the shellfish from restricted areas (heavily polluted sources are excluded by regulation) are transferred to tanks of running seawater in which they are maintained for relatively short periods (24–72 hours) to permit them to open, pump clean water and purge themselves of contaminants. The concept of the process is not new, having been suggested and explored starting late in the last century (Bulstrode 1896; DeGiaxa 1889; Johnstone 1914; Phelps 1911; Fabre-Domergue 1912). The system requires a source of clean seawater, in sufficient quantity to maintain conditions in the holding tanks that will stimulate normal activity in the bivalves being depurated. It is often necessary to treat the seawater to assure that it is free of contaminants so that it does not further contribute to the contamination of the shellfish. The physical facilities required to attain the desired end of maintaining activity and reducing the contaminant load are superficially quite simple, but to function properly they must be designed to conform to rather stringent engineering and operational criteria; details of plant construction and operation are discussed by Furfari (1966), Canzonier (1984) and in the NSSP Manual, Part II, (ISSP 1986).

The process of depuration has often been portrayed by its proponents as the panacea for all types of shellfish contamination. Such is not the case. The efficacy of the process is quite variable, depending on the nature of the contaminant, the species being depurated and the operating parameters which determine the quality of the environment in the holding tanks of a specific plant. Bacterial contaminants, for example, can be quickly unloaded by many species of bivalves during a short sojourn in the holding tanks; viral contaminants, on the other hand, may be released at rates that would render the process ineffective within a reasonable operational time frame for a commercial plant. Indeed, since the titre of bacterial contaminants is the index commonly used to evaluate the efficacy of the depuration process, there are serious shortcomings associated with the use of this process in cases of suspected viral contamination (Richards 1982; Canzonier 1971). The process is also unfeasible to use in the case of very heavy loads of bacterial contaminants (Heffernan and Cabelli 1971). Other types of contaminants (hydrocarbons, heavy metals, biotoxins) may be so avidly sequestered in the tissues of the bivalve that the commercial depuration process is virtually useless in reducing them to acceptable levels. Richards (1988) has recently reviewed the process of depuration in an historical context; his compilation of the literature will serve the reader as a starting point for an expanded examination of this topic.

In addition to the biological limits on the process, it is quite clear that other constraints will apply to the application of depuration. In many areas the individual watermen desire to retain control over their catch up to the point of marketing; depuration on a small scale is not economically feasible, thus a collaborative operation would be required. The use of the process also imposes severe time restraints in marketing procedures and requires the application of very stringent control measures in the handling and distribution of the depurated product; the dealers may find that

these additional requirements, the cost of which must be added to the product, will render the use of depuration economically unfeasible. I have frequently observed that, after establishing a depuration plant, the manager soon discovers that the operational requirements are so onerous that they are either circumvented or the process is abandoned altogether. On the basis of first-hand experience over the past 25 years, I would advise anyone contemplating the application of the process, be they producer, dealer or regulatory agency, to carefully examine the limitations and the potential problems that may arise, before they become excessively enamoured with depuration.

AQUACULTURE SYSTEMS

A question often asked is: . . . . what significance have shellfish sanitation regulations for an aquaculture facility? Clearly, many of the published regulations specifically address shellfish production which utilizes natural populations in open waters. However, the use of even a completely closed system to cultivate or store bivalves will involve some features that come under the purview of the regulations. For example, the source of the culture water, the treatment and storage of the process water prior to and during its residence in the culture system, protection of the system against accidental contamination, handling of the product subsequent to its removal from the system and maintenance of identity of origin are all considerations that enter into the assurance of quality of the product under the NSSP.

Some of the requirements for culture systems are similar to those that apply to the process of depuration mentioned above. Some conditions and operations, however, are unique to aquaculture systems. Unfortunately, and this is due to the rapid development of aquaculture in recent years, there are many aspects of culture operations that have not been adequately defined as regards public health risks. To cite one troublesome example, it is clearly the responsibility of both the FDA and the EPA (or their state equivalents) to monitor and control the use of chemical agents used in the production of animals and plants that enter into the food chain leading to eventual consumption by humans. The culture facility operator might be surprised at the list of substances that fall under the definition of chemical agents and at the elaborate regulatory protocol that must be satisfied to permit their use. Examination of even a simple bivalve hatchery system would reveal numerous chemical agents that are on occasion used to facilitate production. These agents may be used in direct contact with the bivalves in culture, in the treatment of the process water, in the production of natural (phytoplankton) or artificial feeds (microcapsules) or in the construction and maintenance of the physical facilities. Though the quantities of chemical agents typically used render the public health hazard extremely remote, this is an area in which the above agencies have a mandate to become involved. In an attempt to resolve potential problems and reduce negative impacts on a fledgling industry, a nationwide cooperative program referred to as the IR-4, comprising federal (EPA, FDA, Agriculture Research Service) and state agencies (agriculture research stations), as well as representatives of the chemical manufacturers and the operators of the animal production facilities, has been established. Working groups within this program are assigned specific topics to study in detail (mollusc culture is one of these) and then make recommendations for the proper use of chemical agents in various types of production.

There exist some unique problems associated with the maintenance of bivalve molluscs in closed and semi-closed systems. System components may release potentially toxic substances into the process water. Such substance may also be produced within the hydraulic circuit or as an unwanted byproduct of the food production phase, which often involves microbial activity. These "toxic" substances may present no public health risk in minute quantities; however, due to the long holding times associated with growout phases of some systems, they may be accumulated in the bivalve tissues to levels that could raise questions concerning the suitability of the product for human consumption. This type of problem can often be avoided by careful preconstruction planning and by developing a suitable operational protocol for the various phases of production. However, since many aquaculture facilities are essentially prototypes of a unique design, it would be difficult to forsee all problems of this type at the outset. In designing and building a new aquaculture facility, especially if an untried operational protocol will be applied in a new area, it would be prudent to develop the new system in stages so as to permit any necessary changes to be easily and economically incorporated. Fortunately, public health problems associated with aquaculture facilities have not been of significant proportions to date, but this does not mean that they cannot occur.

CONCLUSION

Clearly, the production and marketing of bivalve shellfish involves the application of some rather unique food protection principles. In order to be effective the application of these principles requires the understanding, acceptance and cooperation of the producers and shippers of shellfish; the mere unilateral enforcement of regulations is not enough. Without such a collaborative effort the long-term survival of the industry is severely limited.

Of preeminent importance to the industry is the realization that the primary requisite for assuring a wholesome product is the prevention of the contamination of the shellfish at the source; i.e. production and harvesting in clean waters - the most logical and least onerous approach to applying the principles of shellfish sanitation. Clean growing waters are the *sine qua non* of shellfish production, and shellfish industry members should take an active role in

supporting appropriate provisions for reducing water pollution to levels that will not compromise the sanitary and gustatory quality of their product. Additionally, a workable shellfish sanitation program requires the collaboration of the producers, processors and shippers. Effectiveness of the program in assuring the supply of a wholesome product to the consumer is enhanced when a line of communication is established between the industry members and the regulatory agencies. Indeed, the formulation of realistic sanitary codes can be accomplished only with continued input by the shellfish producers and handlers. The current ISSC operational format permits and encourages such collaboration and industry members are invited to participate in technical sessions and discuss their problems and concerns with the technical and regulatory representatives of the various working groups. This is an excellent opportunity for both sides to learn and to benefit.

ACKNOWLEDGEMENTS

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MITIGATION OF DREDGING IMPACTS TO OYSTER POPULATIONS

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ABSTRACT Maintenance and extensive navaigational dredging in coastal areas along the Northeast and Mid-Atlantic coasts have altered the population dynamics of oysters, *Crassostrea virginica*. In most instances, oyster production has been reduced by removing shell bases and reefs upon which spat could set. One type of mitigation of dredging impacts may be made through a variety of reshelling programs. In Guilford, Connecticut, periodic maintenance dredging since 1957 has been the source of increased mortality of seed oysters and removes the shell base upon which seed oysters set. In 1985, taking into account the Army Corps dredging schedule and seasonal emplacement of private moorings, the Guilford Shellfish Commission acted upon an earlier Sea Grant proposal and made an agreement with a local oyster company to manage oyster bed restoration in this area. Eight thousand bushels of crushed clam shell were planted in 1985 to form a shell base.

In July 1986, 8,000 bushels of clam shell were planted over the shell base which obtained a set of 0-year oysters. A harvest of several thousand bushels of seed oysters was anticipated in 1987. Mitigation agreements which are small in scale and do not interfere with other coastal activities can be expanded to improve oyster resources.

KEY WORDS: *Crassostrea virginica*, dredging, mitigation, natural shell bed, spatfall

INTRODUCTION

The earliest settlers of New England found vast "natural beds" of oysters, *Crassostrea virginica* (Ingersoll, 1881; Goode, 1887; Brooks, 1905), which became a stable and reliable food for many shore communities (Kochiss, 1974). Initially valued as a source of winter sustenance, oyster beds became vital to settlements that eventually became more dependent upon coastal trade for economic survival. Thus, greater attention was focused upon building wharfs and piers. Often, precisely the same areas which first were utilized for fish and shellfish resources were later developed for commercial wharfs. Observations on specific changes in utilization of these estuarine areas, indicated that a discussion of oyster ecology and its impacts upon navigation should be included (Galtsoff, 1964). An example of this is the lower East River in Guilford, Connecticut, which borders the towns of Guilford and Madison. The East River contained a natural oyster bed (Collins, 1889) that was dredged to create a mooring and anchorage area in 1957 (Otis, 1984).

In Connecticut, the natural oyster beds were located in or near river mouths. Often these beds flourished in this brackish environment protected from the severe effects of full-salinity predators such as the starfish. Depending upon recruitment of seed, local oystermen tonged 2,000 to 4,000 bushels of adult oysters in the annually from the East River in 1930s (F. Dolan, pers. comm. 1984). It was commonly stated that "Guilford oysters, taken from the channel of East River, are noted as among the best in Connecticut" (Smith, 1877). In this paper, I report on a study in which a natural oyster bed in the East River continues to reseed itself and in which procedures have been adopted to mitigate damage caused by navigation projects.

Study Site

The East River is located in the eastern part of the Town of Guilford, Connecticut (Fig. 1). It forms much of the boundary between Guilford and the western edge of Madison. The East River is intertidal and exchanges water freely with Long Island Sound around a barrier spit called "Grass Island," also in the Town of Guilford. Its drainage lies mainly to the north and west, consisting of salt marsh, bogs and wetlands. The East River also receives fresh water from the Neck River to the east and from a small tidal creek to the west. The mean tidal range at the mouth of the East River is about 5.4 feet. A long sand bar at the river's mouth identifies it as an ebb channel and is tidal approximately four miles upstream. In 1940, a channel 6 to 12 feet deep and up to 100 feet wide existed at the river's mouth (U.S. House of Representatives, 1941). In 1957, 1,500 feet of the lower East River was dredged to create a mooring area 100 feet wide and six feet deep at mean low water. This mooring area has been maintenance dredged in 1964, 1974 and 1981 (Otis, 1984).

Natural Bed Restoration

The 1957 "improvement" of the lower East River, according to local oystermen, eliminated most of the oyster resources in this area. Oyster sets continued to occur on what few shells remained on shallow bank edges (Walston, pers. comm. 1987). These areas supported a small fishery utilizing tongs until 1966, when pollution closed the river to direct shellfishing (Walston, pers. comm. 1987).

At a February 1984 meeting of the Guilford Oyster Ground Committee, various methods to restore and manage this natural oyster bed, so as not to interfere with boating interests, were discussed. A proposal was made to try to

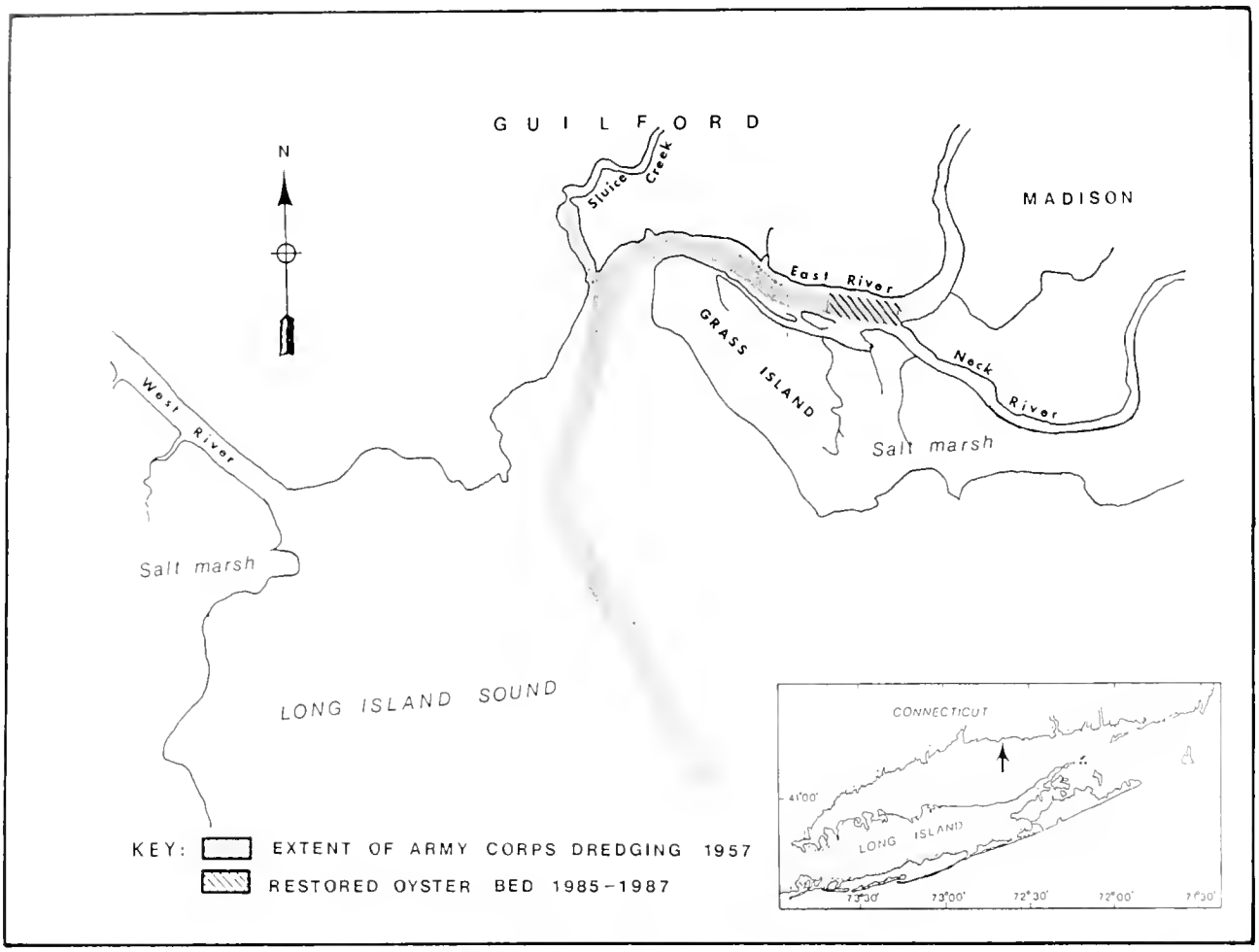

Figure 1. Map of East River Study Site, Guilford, Connecticut

plant cultch in the area for setting purposes but not to allow the growth of oysters to lessen the channel depth and impact navigation.

At a June 12, 1985 meeting of the Guilford Shellfish Commission, Mr. Frank Dolan, a local oysterman, formally requested permission to plant 2,000 bushels of cultch per acre over 12 acres down to the Guilford launch ramp (Minutes of the Guilford Shellfish Commission, June 12, 1985). This area encompassed the entire portion of the federal anchorage in the East River.

METHODS

In late June 1985, Mr. Dolan obtained approval from the Guilford Shellfish Commission to plant cultch in the area 200 feet south of the confluence of the East and Neck Rivers. This cultch planting was followed by additional plantings in 1986 and 1987.

Shell planting was accomplished utilizing an oyster boat belonging to the Dolan Brothers shellfish company. Whole clam shells (*Spisula solidissima*) were selected for their ability to form a firm shell base and obtain an oyster set. By 1987, the section of the East River from the confluence of the Neck River to approximately 400 feet west (about 2 acres) was planted (Figure 1). Permission was obtained from Mr. Dolan to conduct a dredge survey for some clam shells containing seed oysters during the summer.

In July 1987, a hand oyster dredge equipped with a metal pressure plate was utilized to examine shells for seed oysters. This was not an in-depth quantitative study but a presence or absence monitoring survey designed to obtain the number of one- and two-year-old set on a bushel of planted clam shells. To sample the cultched area, five test sites were selected at random. Sampling was accomplished by conducting three one-minute dredge tows over each test site. As each dredge was hauled, all extraneous material, such as glass, leaves and marsh grass, were separated from the clam shell cultch. At each test site shells obtained from the dredge were shoveled into two five-gallon plastic buckets equal to a bushel measure. Each sample was examined for 1985 and 1986 spatfalls. Only oysters attached to clam shells and, therefore, planted were included in the results.

RESULTS

The random sampling previously described yielded many two-year olds and set from last year's spatfall on these shells. The oysters all appeared healthy and growing rapidly. The average number of oysters per bushel of sampled cultch was found to be 74 and ranged from a high of 130/bushel to a low of 27/bushel. No distinction was made between the 1985 and 1986 spatfalls. Several shells contained both year classes and had multiple spat, some up to 10 per shell. It should be noted that from the appearance of the shell surfaces many of the clam shells were partially buried and had formed a shell base. It was not possible to determine to what extent the cultch planted thus far acted as a shell base or as a possible setting surface. Underwater photography of the bed is scheduled in the late fall of 1988 and should show bed configuration and profile. To date, approximately 26,000 bushels of clam shells have been planted.

DISCUSSION

The negative effect of navigation improvements upon oyster resources has been well documented in the scientific literature (Galtsoff, 1964; MacKenzie, 1977). Today, social and economic issues often conflict with various user groups of coastal resources. However, aside from resource allocation decisions, a poor understanding of oyster bed ecology does contribute to reduce oyster production (Visel, 1985).

MacKenzie (1983) states that these natural oyster beds often have deep shell bases, some as deep as 23 feet. John Volk, Chief of the Connecticut Department of Agriculture —Aquaculture Division, has found shell bases to be over 40 feet deep in the Housatonic River in Connecticut (Volk, pers. comm. 1985). These deep shell bases can be attributed to successive oyster generations setting and growing on older oysters, eventually killing them by overgrowth. The elevation of these beds continues to rise and the shells of the dead oysters accumulate underneath, forming the base of the oyster bed. Upward pattern of natural bed development is also discussed at length by Galtsoff (1964) and Brooks (1905). This phenomenon, associated with natural oyster beds in rivers, can significantly lessen channel depths, negatively impacting navigation.

In 1985, the Guilford Shellfish Commission developed a comprehensive plan to address the management of the natural oyster beds within its jurisdiction (Guilford Shellfish Commission Management Plan, 1984). The principal objective of the Guilford Shellfish Commission's new management plan is: "To maintain, over the long term abundant stocks of oysters and clams in order to provide a suitably large fishery for recreational and commercial interests." The program to deepen the channel in the West River with increased oyster harvesting and shell removal and the East River reshelling effort reflect new shellfish management policies. These new policies differed greatly from the traditional regulation of bag limits and restrictions upon gathering methods.

It is evident that a greater understanding of natural oyster bed ecology could provide additional restoration opportunities in many Connecticut municipalities (MacKenzie, 1970). Shell deposits that could be utilized as a cultch source occur in most estuaries (MacKenzie, 1975). In areas of continued oyster setting, on-site reshelling activities should be evaluated. The suitability of pilot projects require the careful review of site specific biological, environmental and social limitations.

It was felt that the East River was a good candidate for a small restoration project; oyster setting was frequent, the Shellfish Commission and the industry both supported the effort and conflicting uses were seasonal. Under no circumstances was the growth of seed and adult oysters to impact upon navigation.

In this case, implementation of new shellfish management policies could possibly eliminate or reduce the need for continued maintenance dredging. If channel depths can be controlled by removing excess oysters or shell, navigation dredging costs would be reduced and the environmental impacts associated with upland disposal of dredge spoils lessened. Follow-up studies of the East River restoration and bed management programs could provide valuable information to other resource managers. Similar small scale projects should be investigated and, in my opinion, warrant further research.

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REHABILITATION OF THE TROUBLED OYSTER INDUSTRY OF THE LOWER CHESAPEAKE BAY

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ABSTRACT After 1885 Virginia's lower Chesapeake Bay system produced more oysters per year than any other area in the United States and remained predominant until 1960. Since then she has surrendered supremacy as annual harvests of her troubled oyster industry have steadily declined. Numerous factors were responsible for the tremendous productivity of the lower Bay's oyster beds; a number have been involved in its decline. Natural events, such as the catastrophic epizootics of the early 1960's, continuing disease and predation, increased salinities of drought years and great freshets of tropical storms have contributed significantly to the reduction. Pollution and other man-related alterations have been involved also. Additionally, high costs of money and operations, risk-reduction efforts, loss of competitive position and markets, and, in some problem areas, lack of certain important scientific knowledge have contributed. Persistent overfishing by public harvesters, lack of application of best-management practices and recent technological advances, reduction of planting efforts by private growers, and resistance to remedial improvements by industry and public managers are the *major factors* causing the continuing decline! Nevertheless, restoration of oyster production in Virginia (and Maryland) waters can be accomplished by applying a combination of currently available scientific knowledge and technological skills and by making or enabling sociological, economic and political improvements.

KEY WORDS: Oyster industry, biological restoration, economic rehabilitation, Virginia, lower Chesapeake Bay.

INTRODUCTION

Since Colonial times the Chesapeake estuarine system has produced the most recorded annual harvests of United States oysters, reaching a high of some 20 million bushels around 1880. During the mid-1800's Maryland's upper Bay and its tributaries annually yielded around 4.9 million bushels of the Atlantic oyster, *Crassostrea virginica*, while Virginia's waters gave up some 2.1 million—less than half (Brooks 1891 and 1905). After 1885, annual catches of the lower Chesapeake surpassed those of the upper Bay and remained predominant until 1960. Since then, Virginia's lower Bay has surrendered its national supremacy and production throughout the entire Chesapeake region has diminished.

The oyster industry of Virginia, long a mainstay of the commercial fisheries supported by the biological resources of the lower Chesapeake, has shown signs of distress since the 1920's. During the decade of the '20's reduced harvests and widely publicized, pollution-related public health problems drove state and federal agencies to investigate the causes of distress. Research programs and organizations, such as cooperative state-federal oyster fishery research programs on the James River, Virginia and at Yorktown, Virginia and the Chesapeake Biological Laboratory at Solomons, Maryland were established for this purpose. Considerable research and engineering development effort has been directed at the oyster fishery in the Chesapeake region and elsewhere since and certain management efforts aimed at increasing production have ensued. As an example of the magnitude of the research and development effort, some 260 related, selected documents have been examined in the course of our studies (Haven *et al.* 1978a and 1978b and Hargis and Haven in press). There are others.

In 1970–71 the present authors undertook an exhaustive study of the Virginia oyster industry which resulted in publication of a monograph (Haven *et al.* 1978a) and an executive summary based upon it (Haven *et al.* 1978b). From these studies remedial recommendations were made to industry, the General Assembly of Virginia and the Virginia State agencies responsible for management of the fisheries and the marine environment. After publication of the main report (Haven *et al.* 1978a), some of the recommendations were adopted partially or wholly, but not enough of them. The key ones have been ignored! The Virginia oyster industry remains seriously troubled.

In 1986 we decided to again review basic conditions of the oyster resources and industry of the lower Chesapeake. The resulting report by Hargis and Haven (in press) is the foundation of this presentation. During this research we learned that several primary problems, the bases of industry's difficulties, have not been effectively addressed in the period since our earlier comprehensive studies. Production of oysters from Virginia's bottoms continues its long-term downward trend.

FINDINGS

Virginia's oyster industry consists of two main elements, the public and private oyster fisheries (Quittmeyer, 1957; Haven *et al.* 1987a and 1987b). Public harvesters are essentially hunters or gatherers, taking seed and market oysters from state (publicly-owned) oyster-growing areas

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within a constitutionally adopted boundary in each tidal estuary and coastal lagoon in Virginia and from the mainstem of Chesapeake Bay—the Baylor Survey Grounds (Figure 1). The private sector consists of oyster planters who, using their own funds, rear and harvest seed and/or market oysters (mostly the latter) on bottoms leased to them by the state. It also includes the oyster shuckers; first-level processors; and, packers and repackers who purchase oysters from public and private harvesters (or from secondary suppliers) for shucking or packing (or both) and for processing to advanced stages for sale and shipment. Shippers, wholesalers and retailers also handle oysters. Some integrated organizations grow, shuck, process, market and ship them.

When all of these elements are considered, the Commonwealth's oyster industry is quite complex (Figure 2). The basic complexity and interwoven nature of various segments of the industry and the economic, social, political and natural factors affecting them at each level complicates effective understanding and management. Indeed, this premise is supported by the results of our review of the current condition of the oyster industry, its problems and promise (Hargis and Haven, in press).

Historically, the oyster industry of Virginia has passed through six phases as follows:

Phase I, the longest (1600 to about 1850), began almost 400 years ago with the establishment of the Virginia Colony. In early Colonial days many oyster reefs extended upward into the water column and were threats to navigation like coral reefs of some tropical waters today. Many were awash at low tide. Surfacing reefs and many submerged ones have long since disappeared. Many now exist only as "reef-shells" buried under a layer of natural and anthropogenic sedimentary overburden. Harvesting of oysters for food, shell and lime; channel dredging; continuing high rates of natural and man-affected sedimentation; sea level increases; and, subsidence have all been involved, with the first most important in the majority of places;

Phase II, beginning around the mid-1800's was characterized by increasing demand for oysters as food and to a lesser extent for building and agricultural materials re-

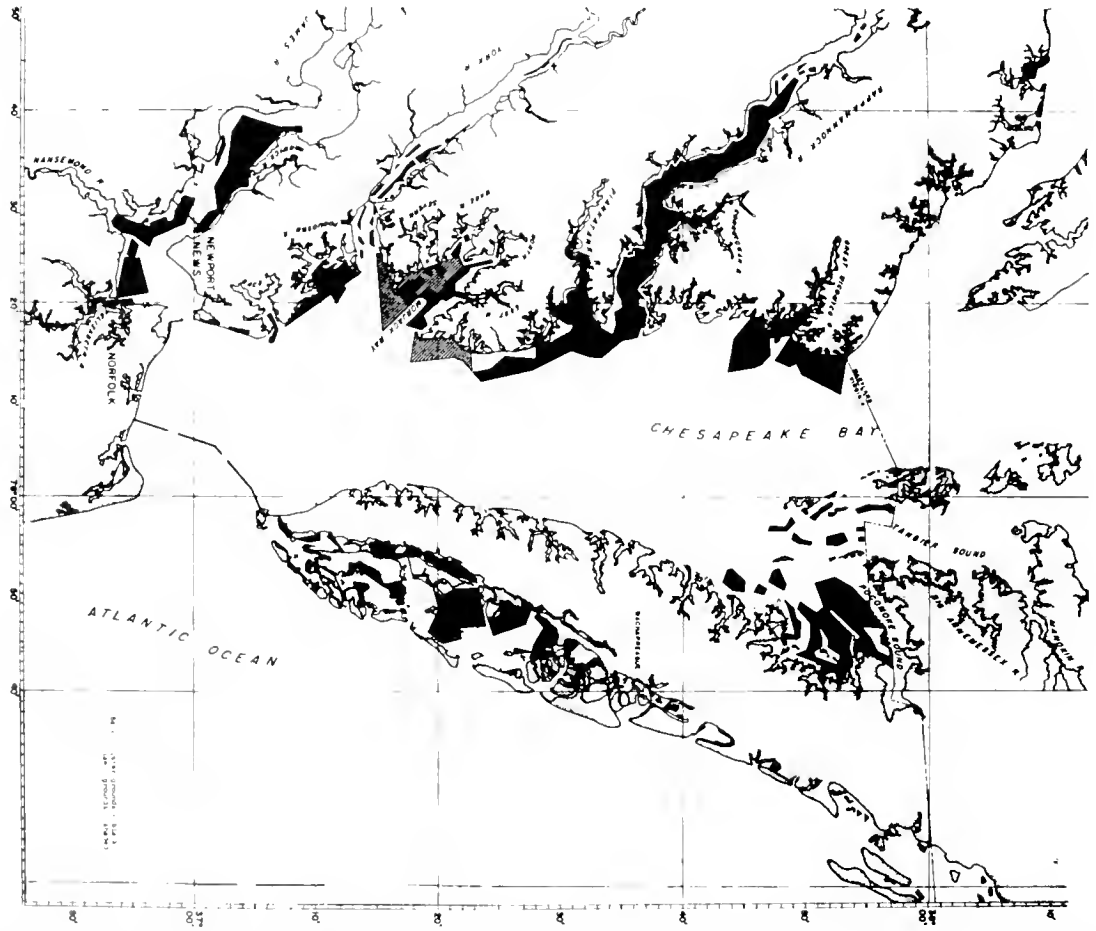

Figure 1. Map of Tidewater Virginia showing public oyster ground and public clam ground. The public oyster ground (Baylor Bottoms—Baylor, 1894) are in black; public clam bottoms are hatched. (From charts on file at Virginia Marine Resources Commission in Newport News, VA)

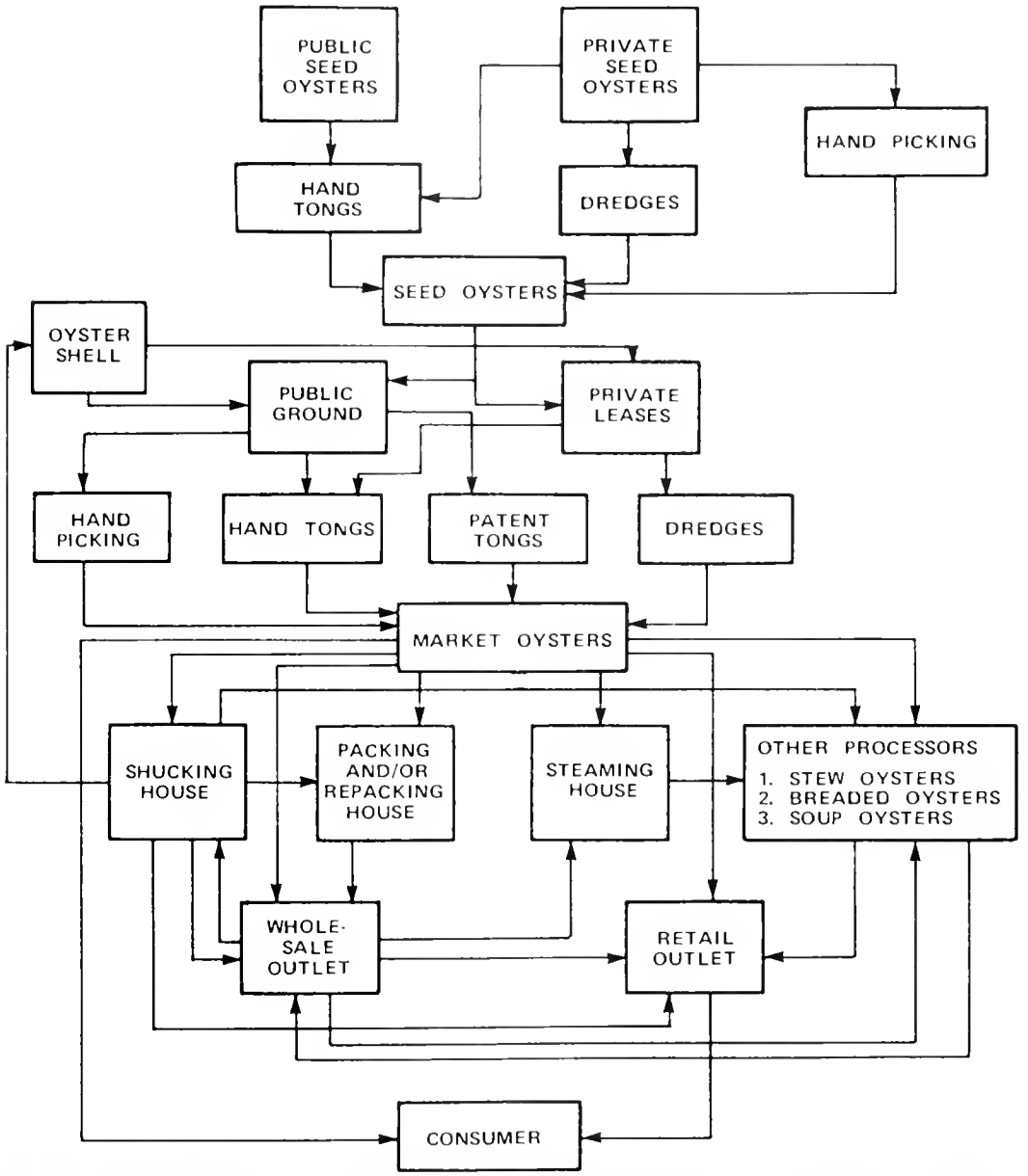

Figure 2. Key elements in the harvesting, processing and distribution of seed and market oysters in Virginia.

sulting from population growth. During this period, market oyster production grew until it reached 6.8 million bushels by 1880 (Table 1);

Phase III lasted from 1894 to 1912 when annual harvests ranged from some 5 to 7.5 million bushels (Table 1). This era can be called the "high water", or peak phase;

Phase IV was characterized by indications of overfishing by the public watermen, and annual harvests from public oyster beds gradually declined during 1913 to 1932. Economic recession prior to and after World War I, the war itself, and overharvesting, may have affected yields or records, or both. In 1925, 4.4 million bushels were taken (Table 1). By 1931–32 annual market-oyster production had declined to 2.4 million bushels (Table 2). [Official record-keeping attained some degree of completeness, continuity, precision, and accuracy only after 1930]. Certainly subsistence oyster fishing for home consumption and local sale occurred during the Great Depression period, but most of those harvests were probably not reported;

Phase V began after 1932 and was characterized by relatively stable landings that reached about 4.0 million bushels for public beds and private leases in the 1958–59 harvesting season [November of one year to the end of October ensuing (Table 2)]. Much of this increase was due to privately financed and managed production from leased bottoms; harvests from public bottoms continued to decline (Table 2 and Figure 3);

Phase VI, extending from 1959–60 to the present (al-

TABLE 1.

Recorded Oyster Landings in Virginia from 1880 to 1925 for Certain Years[a]

Year	Bushels	Pounds of Meats
1880	6,837,320	47,861,240
1888	3,664,433	25,651,031
1890	6,074,025	42,518,175
1891	6,162,086	43,134,602
1897	7,023,848	49,166,936
1901	6,067,669	42,473,683
1904	7,612,289	53,286,023
1908	5,075,000	35,525,000
1912	6,206,098	43,442,686
1920	3,963,569	27,744,983
1925	4,356,416	30,494,912

[a] From Table 16, Haven, Hargis and Kendall (1978a, as modified from Corson, 1930).

most 30 years) was initiated by the suddenly appearing epidemic (epizootic) resulting from the oyster disease known as MSX caused by the protozoan *Haplosporidium nelsoni*. Oysters on the public and private beds in the higher salinity portions of Virginia's Chesapeake system were most severely affected. Harvests from both decreased but the reduction in production from leased ground was catastrophic. Current harvests continue on a downward trend on both types of bottoms (Table 2 and Figure 3).

Operating elements of industry have declined almost 17% (Table 3). In the 1975–1985 decade the shucker-packer segment declined by 36% and shell-stock shippers by 13%. In contrast, repackers and reshippers increased almost 12%.

A major aspect of the recent decline is that while statewide production decreased drastically (by about half) during the period from 1959 to 1964, the reduction in landings was not merely in high salinity, high disease incidence areas, but also in moderate to low disease areas where MSX was not a problem. Following this, statewide total production continued its downward trend and by the 1984–85 season private and public ground production had slipped to only 658,679 Virginia bushels. While the harvests from private, leased beds exceeded those from Baylor (public) bottoms by factors as high as 5–6 times in the 1950's and early 1960's, their comparative positions had all but shifted by harvest year 1977–78. During that year yields from public grounds exceeded those from private leases (512,687 vs. 394,692 Virginia bushels, respectively) for the first time since 1930–31 as they have for 7 of the last 10 harvesting seasons included in Table 2.

For the last 28 years Virginia bottoms have been unable to produce sufficient market oysters to meet the demands of local packers and repackers. Oysters grown elsewhere have filled ever-increasing shares of this need. Oysters, primarily from Maryland (Potomac and Upper Bay waters) in the beginning, then New Jersey, the south Atlantic, and the Gulf of Mexico; and, now from the West Coast, have been imported to supply the Virginia industry. It is reported that the Pacific oyster, *Crassostrea gigas*, is now being processed or repacked by some Virginia packers and sold in local supermarkets as "fresh oysters". The slight growth in repackers and reshippers is the only reversal of the overall downward trend in numbers of oyster-handling organizations (Table 3). This probably reflects the increased importance of imports to the Virginia oyster industry while the reduction in the shuckers-packers and shell-stock shippers organizations reflects the declining availability of locally grown oysters.

The factors responsible for the 28-year decline in oyster production from Virginia waters are many and intertwined. Continuing overfishing of public oyster beds, catastrophic epizootics, fresh-water kills, lowered levels of brood-stock, reduced setting and continuous predator pressure are definite causes. Declining environmental quality is strongly suspected as a contributor in certain heavily populated and industrialized areas, such as the lower James River. Economic elements have contributed to rising production costs. These include increasing costs of money (during the last 20 years), availability of higher economic yields at less risk in other investment areas, generally stagnant dockside prices, consumer resistance and competition from harvesters and growers outside of the State. Failure of the public sector to adjust to modern production methods, and inadequate public and private management have also contributed.

With so many factors operating it is difficult to separate or rank them objectively. First, all facets are not equally understood and for some further study and analysis is needed; secondly, some can never be evaluated separately because of their intertwined nature. Yet clarification is possible!

Overfishing has been identified as the single most important factor affecting yields from publicly owned and "managed" Baylor Survey Grounds (Haven *et al.* 1978a and 1978b; Hargis and Haven, in press). Oystermen have consistently taken more market oysters from public bottoms than were replaced under prevailing conditions and management practices since the early 1900's. When more market-sized oysters consistently are taken than nature and management can replace, overfishing is the inescapable conclusion (Tables 1 and 2 and Figure 3)!

Reduction of planting by private, oyster-growing leaseholders in the wake of the MSX epizootic clearly was responsible for most of the drastic decrease in total oyster production since 1959–60 (see Table 2 and Figure 3). Persistent low-levels of oyster production from leased beds continues because investments in new plantings are withheld. The disease outbreaks of late 1986 and 1987, an extremely dry period that resulted in salinity increases in the Bay waters and caused spreading, disease-related mortali-

TABLE 2.

Virginia Market Oyster Production from Public and Private Bottoms, and Total Landings, in Virginia bushels for the Harvest Years 1930–31 through 1986–87[a,b]

	Public[a]	Private[b]	Total
1930–31	1,017,641	1,830,836	2,848,477
31–32	991,335	1,404,952	2,396,287
32–33	934,537	1,402,231	2,336,768
33–34	1,155,640	1,689,860	2,845,500
1934–35	1,028,023	1,871,116	2,899,139
35–36	565,824	1,993,418	2,559,242
36–37	598,345	1,230,304	1,828,649
37–38	619,407	1,459,308	2,078,715
38–39	733,871	1,834,298	2,568,169
1939–40	824,383	2,059,271	2,883,654
40–41	726,241	2,092,864	2,819,105
41–42	606,498	1,797,363	2,403,861
42–43	749,410	1,857,321	2,606,731
43–44	845,721	1,338,603	2,184,324
1944–45	634,179	1,906,500	2,540,679
45–46	997,843	2,346,535	3,334,378
46–47	1,060,147	1,953,155	3,013,302
47–48	962,284	2,517,992	3,480,276
48–49	1,015,035	2,423,447	3,438,482
1949–50	586,412	2,034,097	2,620,509
50–51	444,4741,969,207	2,413,681	
51–52	374,013	2,259.970	2,633,983
52–53	419,063	2,372,742	2,791,805
53–54	510,333	2,951,485	3,461,818
1954–55	517,178	2,766,137	3,283,315
55–56	650,333	2,820,314	3,470,647
56–57	592,181	2,601,353	3,193,534
57–58	586,304	2,926,750	3,513,054
58–59	703,915	3,347,170	4,051,085
1959–60	699,420	2,553,275	3,252,695
60–61	781,783	2,237,736	3,019,519
61–62	227,921	1,815,001	2,042,922
62–63	278,830	1,652,880	1,931,710
63–64	576,857	1,223,549	1,800,406
1964–65	615,864	1,605,759	2,221,623
65–66	605,982	1,188,633	1,794,615
66–67	226,855	587,105	813,960
67–68	262,996	790,483	1,053,479
68–69	227,577	621,463	849,040
1969–70	192,187	818,943	1,011,130
70–71	281,001	836,014	1,1170,15
71–72	260,241	928,404	1,188,645
72–73	157,890	394,121	552,011
73–74	374,522	424,277	798,799
1974–75	403,737	491,860	895,597
75–76	397,209	475,159	872,368
76–77	312,539	320,711	633,250
77–78	512,687	394,692	907,379
78–79	590,533	441,082	1,031,615
1979–80	608,880	465,896	1,074,776
80–81	704,848	472,465	1,177,313
81–82	464,280	326,809	791,089
82–83	329,492	361,792	691,284
83–84	241,517	285,777	527,294
1984–85	341,757	316,922	658,679
85–86	328,338	386,665	715,003
86–87	273,811[c]	265,695[c]	539,506[c]
	(476,050)[c]		(741,745)[c]

[a] Public Harvests: Landing data for 1930–31 to 1962–63 and 1975–76 through 1976–77 are from NMFS *Fisheries Statistics of the U.S.* Essentially, they are the same as shown in Table 13 (Haven, Hargis, Kendall 1978a).

Data for 1965–66 to 1976–77 were obtained from the annual summaries of the VMRC. They are mostly the same as shjown in Table 12 (Haven, Hargis and Kendall 1978a).

Data for 1977–78 to 1986–87 were calculated from current Virginia Landings (VMRC Newport News, Virginia).

[b] Private Harvests: Landings data for 1930–31 to 1962–63 were from NMFS (*Fisheries Statistics of the U.S.*). They are the same as shown in Table 13 (Haven, Hargis and Kendall 1978a) and are the best available despite certain shortcomings.

For 1965–66 to 1974–75 they were obtained from the annual summaries of the VMRC, Newport News, VA.

Landing data for 1975–76 to 1976–77 were calculated from Va. Landings NMFS (on the basis of pounds landed).

Data for 1977–78 to 1985–86 were calculated from Va. Landings VMRC, Newport News.

[c] During the 1986–87 harvest year the James River seed bed area became the major source of market oysters (called "clean culls" there) and Virginia Landings showed that a total of 476,050 Va. bu. had been taken from public bottoms in Virginia. This figure is shown in parentheses for emphasis! This was a marked increase (147,712 Va. bu., or some 45%) over the 1985–86 market oyster harvest of 328,338 Va. bu. from public rocks. However, VMRC records for 1986–87 (*i.e.* VMRC computer files on 2.4.88) show that many of the publicly taken market oysters for that harvest year (some 202,239 Va. bu., or 42.5%) had come from the James River, mostly from the traditional seed beds. Since harvest of large quantities of market oysters from these beds was unprecedented, any comparison of the market oyster yields of 1986–87 (and 1987–88, when finally in) with earlier harvests must take this into account to be as accurate and realistic as possible!

Actually, the market yield datum for the 1986–87 harvest most comparable with those of previous years was 273,811 Va. bu (*i.e.* the first number presented in the table for harvest year 1986–87) since the clean cull (market) harvesting from the James River seed beds had not begun in earnest before 1986–87 (though up until the Kepone incident of late 1975 small oysters for use in preparation of soup, stew and chowder, called "soups", which may have been recorded as market-oysters or clean-culls, had been taken from some beds in the lower James). Compared with the 1985–86 yield of 328,338 Va. bu. of market oysters from public bottoms this represents a reduction of some 54,527, or 16.65.

Total non-James market oysters production of 539,506 Va. bu. represents the *second lowest yield of record* since the 1930–31 harvest year when more-or-less "careful" recording of harvest first began, 57 years previously. It exceeded only slightly (12,212) the 1984–84 harvest of 527,294 Va. bu., which was the lowest! Compared with the total of 715,003 from 1985–86 this is a decrease of 175,497, or 24.5% — nearly a quarter. This remarkable reduction, related mostly to the inroads of disease, previous over-harvesting and transfer of most of the hand-tonging harvesting effort to the James River seed beds continues the dismal story of decline of yields from the non-James public bottoms.

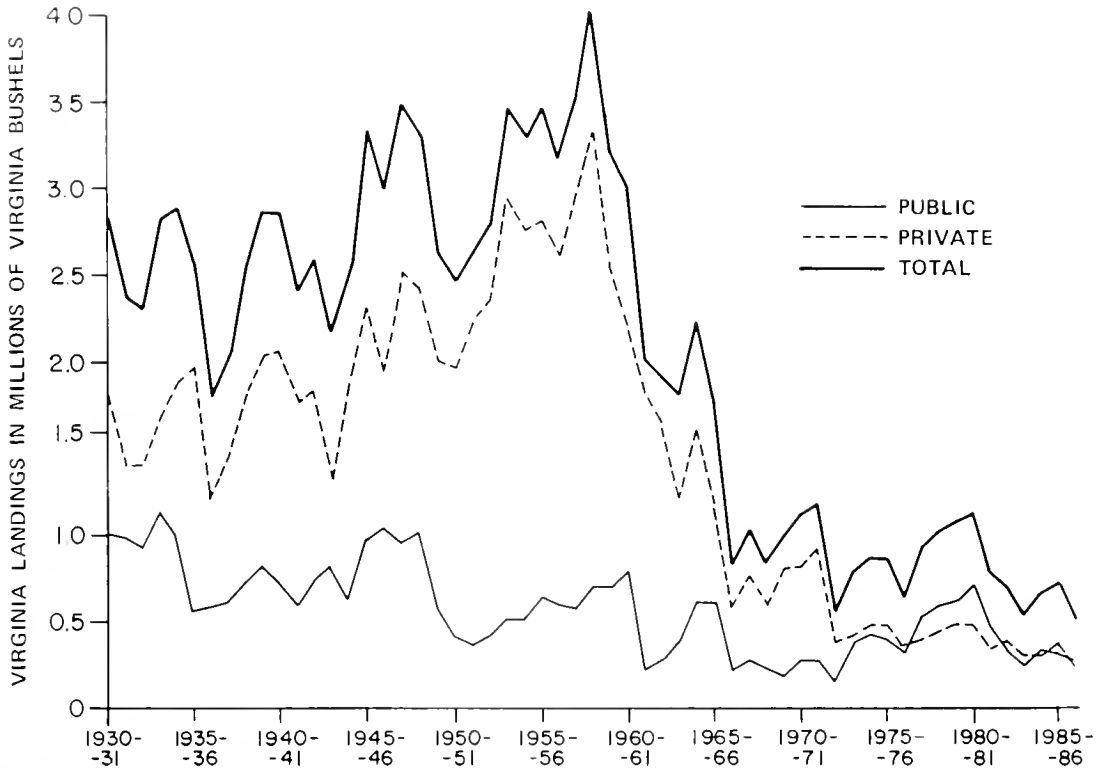

Figure 3. Annual reported market-oyster harvests from public and private beds of the lower Chesapeake Bay from the 1930–31 through the 1986–87 harvest years.

ties (even in Maryland's upper Bay according to George Krantz, personal communication), have further damaged oyster production by private growers almost everywhere and on non-James River public bottoms.

RECOMMENDATIONS FOR RESTORATION

Despite these serious difficulties, we are firmly convinced that marked improvement in production of market and seed oysters within a reasonable period (5–10 years) is possible and that every effort should be made toward revitalizing the private and public sectors of the industry! The Commonwealth will benefit.

Sufficient scientific and technological knowledge is now available for reversal of the long-term decline in market and seed oyster production even though more is needed to restore the fishery to pre-1920 levels of production and to enable industry to cope with changing environmental and economic conditions. Critical management recommendations are:

A. To increase oyster production from Virginia waters:

1. By the private sector (at its own and not public expense)—

Of the some 243,000 acres of Baylor Survey Grounds, most of which are of much better oyster-producing potential than those acreages now available for leasing, only a small fraction (*i.e.* less than 10%) is "managed" by the State in its repletion programs. The rest are largely unproductive or only marginally productive. Leases to private growers of some of the acreage with higher producing potential would reduce the risks of losses and increase possible yields. Opportunities for higher production than the historical 1:1 seed to market oyster yield (the norm as we have discovered) would help encourage oyster planters to make greater investments in plantings for market oysters. Hence, to speed revitalization of private oyster production, we recommend strongly that a reasonable portion of the better quality unused public oyster grounds with potential for higher yields be identified by the state and opened up to carefully-controlled leasing.

2. By the public sector—

State managers must immediately establish appropriate

TABLE 3.

Numbers of oyster-handling businesses in Virginia in 1975 and 1985 by permit category

	1975	1985
Shuckers–Packers	83	53
Repackers	46	51
Reshippers	0	1
Shell-Stock Shippers	54	47
Total	183	152

regulations and undertake enforcement measures necessary to reduce harvests from public bottom. The goal should be to balance harvesting pressure with the recruitment capabilities of the grounds, providing continuing yields without stock depletion.

To increase market oyster yields as harvesting pressures and natural productivity are equalized, public bottoms must be actively and forcefully cultivated. In general, more effective applications of suitable cultch materials are required for more and better quality substrate to increase spatfalls. Shell (or other suitable cultch) must be planted at places where and when maximum sets are expected to occur, not where local political pressures are strongest or when shell is cheapest. Unproductive shell plantings are a waste of effort and money and accomplish nothing of lasting value. Seed should be planted regularly on those areas where local spatfall is usually inadequate but growth and survival are suitable.

Further, a better system insuring effective closure of grounds to harvesting while production is being rejuvenated is also important. Generally, present practice by VMRC managers allows harvest even before remedial measures become effective.

B. Improvement in seed supply is vital to increasing the market oyster production by private and public sectors. This can be done by:
   1. Improving seed yields from public seed bottoms in the James River by more effective application of traditional cultch for spatfall, *i.e.* planting the cultch at favorable times and places and in desirable amounts. Further, existing cultch may be improved by "turning" or other "resurfacing" methods. Suitable alternate cultches such as surf-clam, ocean scallop, ocean quahog and hard clam shells could be useful.
   2. Closure of seed oyster producing areas to all competing uses except seed production until the beds recover and become self-sustaining and while demand for seed remains unmet. The present practice of allowing market oyster production from vital James River seed areas should be discontinued until a sound long-range management plan is in place.
   3. Developing and maintaining other areas (*i.e.* the Piankatank and Great Wicomico Rivers) as supplemental and backup seed sources, using the same management techniques outlined above.
   4. Making suitable acreages of the public bottoms in the James River seed area, the Piankatank and the Great Wicomico available to private growers as sites for seed production.

      [Seed and market leases should be carefully identified and apportioned, controlled and monitored by the Virginia Marine Resources Commission (VMRC), the public fisheries management agency, as should its own public market and seed-growing acreages.]
   5. Continuing production-level hatchery operations to enhance natural seed production and provide back-up support should wild seed production falter and, especially, to produce rehabilitative brood-stock and seed with desirable disease-resistance and growing capabilities.

These recommendations, if followed, should enable the public and private sectors of Virginia's oyster industry to increase productivity. Nothing should be allowed to deter or delay their adoption or continuation! More detailed recommendations aimed at bringing about this objective are provided in Hargis and Haven (in Press). In the meantime, our extensive monograph (Haven *et al.* 1978a) and the shorter Executive Summary (Haven *et al.* 1978b) are available in many institutional libraries.

Making the assumption that long-term rainfall and salinity patterns, and hence disease-levels, will return to the Bay watershed, we are convinced that seed and market oyster production from the lower Chesapeake Bay can be increased to early 1950 levels within five to ten years by adoption of essential public and private management measures based upon current scientific knowledge and seed and market oyster-producing technology. Several other remedial measures are necessary to increase production even more and ensure growing and improved yields over the long-term:

1. Though there are other factors such as currently high levels of disease, which we assume will subside as weather and salinity patterns return to normal, the major limitations to improving seed and market oyster production in Virginia in both the short and long-term future are economic, sociological and political understanding and engineering.

   Overharvesting by fishermen, resistance to more efficient and effective management measures and the *lack of will, purpose or incentive* by public legislative and executive resource and environmental managers to effectively control the oyster fishery, the resources on which it is based and the environment on which the resource depends are the major factors responsible for the continuing decline of Virginia's oyster resources and its industry (as they are elsewhere). Since these factors are so important, sociological and economic research would seem paramount! Accordingly, we place a high priority on soundly conceived and conducted sociological, sociopolitical and socioeconomic studies directed to more effective public and private management of the fisheries, the environment and the oyster resources. They should be done and acted upon quickly.
2. Development of more thorough and useful understanding of the environmental factors (natural and

man-influenced) responsible for low levels of larval setting (i.e. low setting) and high spat mortality and the converse—adequate or high setting and survival of seed and market oysters. These include more careful studies of environmental and physiological requirements of larvae, spat and adults, the lethal and sublethal effects of contaminants and the factors affecting setting and survival.

3. Developing more effective techniques of accommodating to, avoiding, preventing or treating the diseases affecting larval, juvenile and market oysters. Major diseases in Chesapeake Bay and Seaside of Virginia are MSX caused by (*Haplosporidium nelsoni*), SSO (*H. costalis*) and "Dermo" (*Perkinsus marinus*).
4. Improving the technology for acquiring new supplies of cultch and in using existing supplies more effectively. Research should include searches for untapped stocks of reef-shelf near growing areas, use of ocean quahog, sea scallop, surf clam, hard clam and other natural cultch and promising artificial cultch. Cultch existing on the beds can be enhanced by proper manipulation to reduce fouling at setting time. Survival of spat can be improved by proper seed management.
5. Understanding, accommodating to and/or controlling predation from oyster drills (*Urosalpinx cinerea* and *Eupleura caudata*), blue crabs (*Callinectes sapidus*), cow-nosed rays (*Rhinoptera bonasus*), oyster leeches (*Stylochus ellipticus*) and others in the Chesapeake and on Seaside. These predators remain actual or potential deterrents to an increase of oyster yields to maximum levels, are sources of biological and economic losses and, as oyster production is restored, will certainly increase their tolls.
6. We have recommended increased support of experimental seed oyster hatcheries and controlled stock-improvement research already underway at VIMS. The State should also encourage industry to participate in this activity through its own research and development programs and by continuing to provide effective advisory service programs. Industry should be encouraged to modernize in this and other ways.

CONCLUSION

In summary, after reaching a peak of 7.6 million recorded bushels in 1904, market oyster production in Virginia's Bayside (lower Chesapeake and its tributaries) and Seaside waters has steadily declined to current levels of less than 1 million Virginia bushels. While diminishing environmental quality may have been a factor in this 80-year decline and must be attended, other factors (such as still poorly understood outbreaks of MSX, SSO, and Dermo, predators, natural catastrophes, adverse economics and continuing poor oyster-production statistics) have also taken their toll. Most of these problems have been recognized widely for some time and, under normal climatological, hydrographic and economic conditions, can be dealt with.

The largest single factor responsible for the continuing downward trend is *overharvesting!* The Virginia oyster industry has been living off of the principal of its oyster producing potential and not the interest for almost a century! The State and the industry, especially the public sector of industry, have been unwilling or unable to recognize this fact, or—if it has been recognized, able to effectively ignore it. Many have continued to resist adoption of more effective management measures, again and again, for whatever short-sighted reasons they have advanced for short-term financial or political gain.

As always, overharvesting is relative. Prevention of continued decimation of oyster stocks (existing principal) requires a reduction of harvesting effort (withdrawals of interest) to maintain present stock levels and allow addition of new stocks (new principal). No person, government, institution or industry can continue to deplete principal without eventually running out of it, and destroying the possibility of future interest yields (harvests). Yet we are doing precisely that. The handwriting is on the wall. Put simply, if public and private oyster-producing efforts continue as they are, Virginia's position as a significant producer of oysters will decline even further!

To increase yields, more stringent and effective management measures for the public oyster beds are needed—now! If they are not brought about quickly, public and private oyster production will continue to decline to some lower, less valuable but sustainable level and a large portion of the oyster industry based upon Virginia-grown oysters will disappear as some has already. But it need not do so! Production from Virginia bottoms can be increased significantly within the next 5 to 10 years if the essential management steps recommended above are taken quickly and effectively!

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MANAGEMENT OF OYSTER RESOURCES IN APALACHICOLA BAY FOLLOWING HURRICANE ELENA

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ABSTRACT The Florida Department of Natural Resources conducted resource assessments following Hurricane Elena (September 1985) to determine the storm's impact on commercially valuable oyster reefs along Florida's northern Gulf Coast. The Apalachicola Bay system, Franklin County, was identified as most severely damaged. Oyster production was reduced to levels which would not support commercial harvesting. A comprehensive management plan was developed to protect surviving resources, mitigate economic hardship, and promote resource recovery. Field surveys identified resource losses, monitored recovery, and predicted production. Specific areas were opened to harvesting eight months after the storm when stocks reached levels which could sustain limited harvesting. A redefined regulatory strategy limited harvesting times, established bag limits, and required that harvesters pass through checkpoints before landing their catch. Additionally, cooperation between federal and state agencies produced successful programs to sustain the shellfish dependent economy and promote long range resource benefits. Nearly $2 million were allocated for restoration of 400 acres of damaged reefs.

KEY WORDS: Oysters, resource management, Apalachicola Bay, Hurricane Elena, resource recovery.

INTRODUCTION

Extreme environmental and meteorological conditions associated with Hurricane Elena were expected to have had deleterious effects on shellfish resources along the Northern Gulf Coast of Florida. Coastal areas experienced extreme tides, hurricane force winds, and heavy rainfall while the storm was located in the eastern Gulf of Mexico from 29 August through 2 September 1985 (Balsillie 1985). In response to the storm's anticipated adverse effect on oyster resources, the Florida Department of Natural Resources initiated an assessment of damage to commercially important oyster reefs.

Preliminary assessments of oyster producing areas identified Apalachicola Bay, Franklin County, as most severely impacted. Apalachicola Bay contains Florida's most commercially productive oyster reefs and was the source of 92% of the oysters landed in the State in 1984. Resource assessments following the storm indicated oyster populations on principal producing reefs in eastern Apalachicola Bay were reduced to levels which would not support commercial harvesting. Reefs in western portions of the Bay were less severely affected, but oyster populations were limited and would not sustain concentrated commercial exploitation. Due to estimated reductions in potential oyster production from reefs scheduled to open for the Winter harvesting season (1 September through May 31) and the potential for injurious over-exploitation, the Department of Natural Resources prohibited oyster harvesting from the waters of Franklin County on 11 September 1985.

The economic consequences that would result from an extended closure of Apalachicola Bay made it imperative that oyster harvesting begin as soon as stocks recovered sufficiently to sustain commercial harvesting. A comprehensive management plan was developed, including resource assessment, specific regulatory mechanisms, and mitigative programs to permit harvesting while promoting resource recovery. Resource assessment was critical to evaluating resource availability, predicting production, and monitoring recovery. A resource assessment program begun in 1982 was used for baseline data on oyster population dynamics. Emergency measures to regulate oyster harvesting also provided an opportunity to monitor landings and harvesting pressure. Resource restoration programs were implemented to accelerate recovery of reefs which were severely damaged.

METHODS

A field survey program was established in 1982 for resource assessment and additional stations were included following Hurricane Elena (Figure 1). The number of stations on each reef ranged from one to four. Five quadrats were selected randomly at each station. Quadrats were considered random since all reefs were subtidal and oyster densities and distributions could not be determined from surface observations. A weighted 0.25 m^2 PVC grid was used to delineate sample quadrats. Samples were collected by divers; all live oysters, shell, associated fauna, and debris were removed to a depth of 15 cm, placed in mesh collecting bags, and delivered to the survey vessel. Live oysters were measured to the nearest lower 0.5 cm length (longest dimension). Substrate characteristics, shell volume, predators, competitors, and freshly dead oysters (boxes) were noted.

Length frequency distributions were developed for field surveys during each sampling interval. Standing stocks were estimated from oysters collected from 0.25 m^2 quadrats. The percentage of oysters equal to or greater than 75 mm provided estimates of harvestable oysters/m^2 which were extrapolated to calculate production levels. Produc-

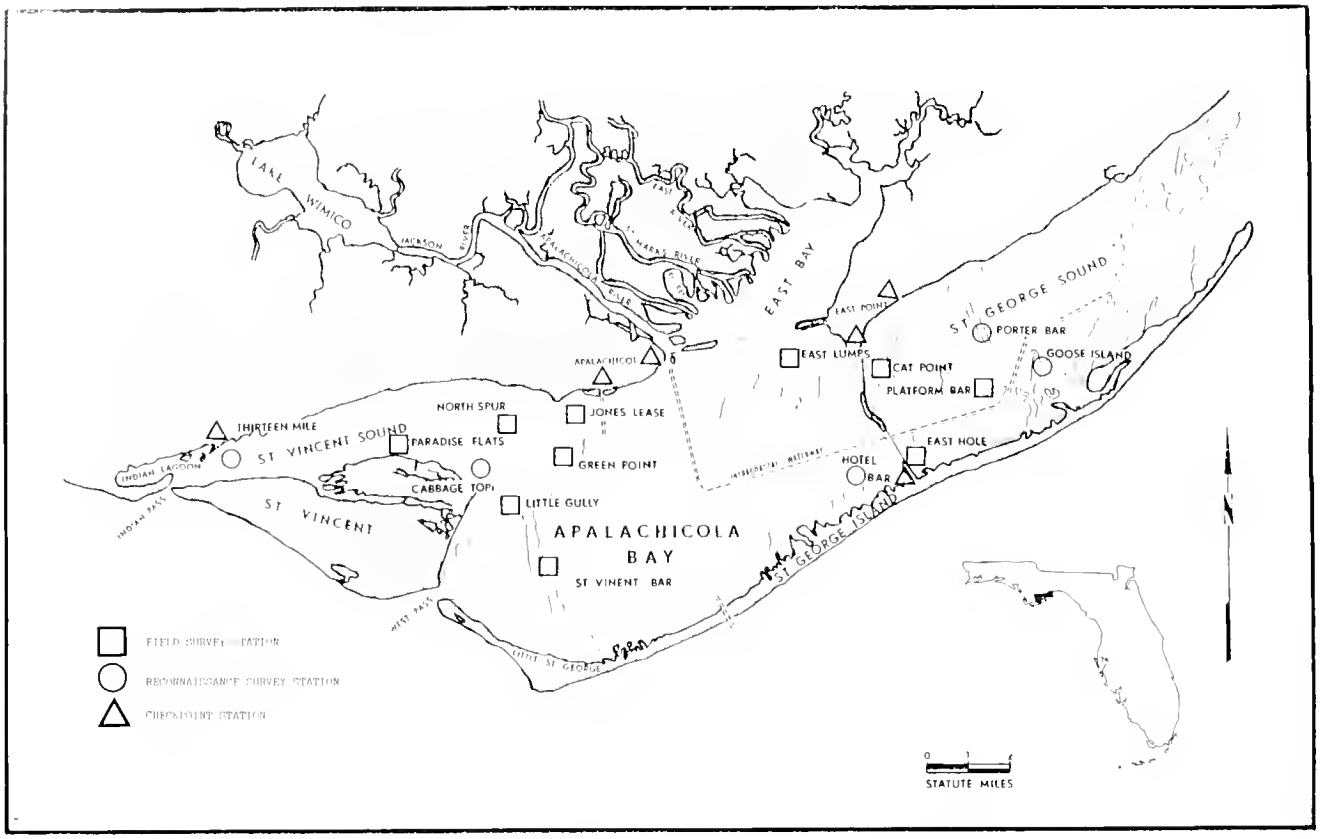

Figure 1. Location of field survey stations and checkpoints in Apalachicola Bay.

tion levels were also defined as bags/acre, where the capacity of a bag was 225 oysters.

Checkpoints were established to monitor harvests before oysters were delivered to certified shellfish dealers. Daily harvests, number of vessels engaged in harvesting, and catch per vessel were monitored. Harvesting rates were important indicators of resource depletion and recovery.

Programs were initiated to restore damaged oyster reefs and mitigate adverse economic impacts. Programs funded by State legislative appropriations were directed to employ oystermen to transport and plant live oysters and shell to rehabilitate oyster reefs. A second program, to restore severely damaged oyster reefs, was implemented using emergency assistance funding through the Commercial Fisheries Research and Development Act, Public Law 88-309(4B). Severely damaged reefs were restored by dispersing clam shell across degraded reef surfaces. Reefs restored during this program were designated as Special Resource Recovery Areas where additional protective measures were applied.

RESULTS

Post-Storm Structural Damage

Preliminary assessments indicated reefs lying in eastern portions of the Apalachicola Bay System, specifically East Hole, Platform Bar, and Cat Point, were severely damaged by Hurricane Elena. Shellfish habitat on East Hole and Platform Bar sustained the greatest damage; practically all harvestable oysters were eliminated. Damage was less extensive in eastern portions of Apalachicola Bay and in St. Vincent Sound.

Structural integrity of an oyster reef can be described as the discrete and contiguous assemblage of live oysters and oyster shell which form the substrate for a complex benthic estuarine community. Hurricane Elena severely disrupted structural components of reefs in St. George Sound, resulting in extensive habitat destruction, disruption of reef ecology, and loss of production. Oyster shell (cultch), which forms the integral framework of productive reefs, was often removed or buried, reducing once productive reefs to less productive compacted flats.

Structural damage was characterized by several types of degradation, including transport and deposition of shell and sediment, scouring, and abrasion. Assessments of reefs indicated structural damage was variable, depending on the number of adverse factors affecting individual reefs. Based on observations of the most severely damaged reefs, it was hypothesized that shell and live oysters were apparently suspended while the substrate was fluidized by turbulent hydraulic activity. Suspended material was subsequently transported across reefs and deposited on soft sediments

which could not support live oysters, or settled on firmer substrates but was buried by deposition of finer suspended material. The presence of blackened shell on reef surfaces indicated turbulence was severe enough to expose shell previously buried deeply in anoxic substrata. Reef surfaces were also compacted by wave action and deposition of sand and fine shell fragments which covered live oysters and larger shell. Exposed shell on reef surfaces was cleaned and fouling organisms were conspicuously absent.

Severe structural damage also resulted when deposition of sand was extensive. Depositional damage was characterized by the presence of smooth compacted layers of sand and fine shell fragments over reef surfaces. Reefs adjacent to extensive sources of sand were most vulnerable to depositional degradation. Sand was transported from shoals in eastern St. George Sound and from St. George Island to nearby reefs.

Reefs in eastern Apalachicola Bay were impacted by turbulence which suspended and scoured reef materials, but transport of live oysters and shell off reefs and deposition of sand were less extreme. Severity of structural damage diminished on more westwardly located reefs. Structural damage ranged from marginal to minimal on reefs in western portions of Apalachicola Bay and St. Vincent Sound. There was minimal evidence of scour, suspension and deposition of reef material, or disruption of reef ecology.

Surviving Oyster Populations

Production from St. George Sound is critical to the oyster industry, and even moderate declines would cause severe economic constraints. Estimated production on East Hole was reduced to 20 bags/acre, far below levels necessary for commercial viability (Table 1). Estimated production levels for Cat Point dropped below 100 bags/acre compared to 444 bags/acre immediately before the storm. Annual production estimates for Cat Point during September for years 1982 through 1985 ranged from 289 to 634 bags/acre; average estimated production exceeded 450 bags/acre. Surviving oyster populations on Cat Point were reduced from 76 to 23 oysters/m^2 (Table 2). Surviving populations on Cat Point were expected to exert the greatest stabilizing influence on short-term production since Cat Point and contiguous reefs make up the Bay's largest and most productive reef. Population losses were less extensive on reefs located in western Apalachicola Bay and St. Vincent Sound. However, estimated production levels (<200 bags/acre) and limited available acreage were not adequate to sustain harvesting if fishing effort was concentrated on these reefs.

Recruitment to Harvestable Stocks

First spatfall following the storm occurred during the last two weeks in September 1985. Additional setting was observed well into November, when water temperatures

TABLE 1.

Population estimates for oysters on Cat Point and East Hole before and after Hurricane Elena.

Cat Point Field Surveys							
Date	Samples No.	Oysters (n)	Mean (mm)	% >75 mm	Oysters/m^2	Oysters >75 mm/acre	Bags/acre
5/85	20	378	57.6	17.5	76	53,825	239
8/85	11	209	64.2	32.5	76	99,961	444
9/85*	26	147	60.9	22.5	23	20,943	93
10/85	20	161	61.1	26.1	32	33,801	150
11/85	20	571	32.3	4.4	114	20,300	90
1/86	10	680	33.9	4.6	272	50,636	225
3/86	20	2828	34.3	2.4	566	54,974	244
5/86	15	2768	41.7	2.4	738	71,680	319
8/86	20	1884	54.0	10.0	377	152,572	678
9/86	20	1759	58.8	21.2	352	302,003	1342
East Hole Field Surveys							
Date	Samples No.	Oysters (n)	Mean (mm)	% >75 mm	Oysters/m^2	Oysters >75 mm/acre	Bags/acre
9/84	5	132	55.7	18.2	106	78,075	347
12/84	5	215	63.3	25.6	172	178,198	792
5/85	20	286	56.2	15.7	57	36,217	161
9/85*	7	11	55.9	18.2	6	4,419	20
10/85	15	15	67.3	40.0	4	6,475	29
11/85	15	28	60.9	25.0	7	7,082	31
1/86	5	627	26.7	1.0	502	20,316	90
9/86	15	1689	60.7	33.9	450	617,370	2744
12/86	10	916	65.5	40.7	366	602,849	2679

* Hurricane Elena

TABLE 2.

Population estimates for oysters surviving Hurricane Elena on Cat Point and East Hole.

Date	Samples No.	Oysters (n)	Mean (mm)	% >75 mm	Oysters/m²	Oysters >75 mm/acre	Bags/acre
Cat Point Field Surveys							
5/85	20	378	57.6	17.5	76	53,825	239
8/85	11	209	64.2	32.5	76	99,961	444
9/85	26	147	60.9	22.5	23	20,943	93
10/85	20	161	61.1	26.1	32	33,801	150
11/85	20	123	59.2	21.1	25	21,348	95
1/86	10	61	72.2	50.1	24	48,661	216
3/86	20	105	79.0	63.8	21	54,222	241
5/86	20	97	82.8	76.3	19	58,669	261
8/86	20	71	82.9	83.1	14	47,082	209
9/86	20	52	85.0	92.3	10	37,759	166
East Hole Field Surveys							
12/84	5	215	63.3	25.6	172	178,198	792
5/85	20	286	56.2	15.7	57	36,217	161
9/85	7	11	55.9	18.2	6	4,419	20
10/85	15	15	67.3	40.0	4	6,475	29
11/85	15	28	60.9	25.0	7	7,082	31
1/86	5	15	65.0	40.0	12	19,425	86

cooled. Extensive spat settlement was reported on all oyster reefs in eastern Apalachicola Bay. Oyster length frequency distributions after the storm demonstrated significantly higher recruitment than observed during the same periods in 1982, 1983, and 1984 (Berrigan 1987).

Recently settled juveniles commonly reached a length of 25 mm in 12 weeks and 45 mm in approximately 28 weeks (Table 3). Fastest growing oysters on East Hole reached 60 mm in 13 weeks; on Cat Point the fastest growth recorded was 65 mm in 21 weeks. Ingle and Dawson (1950) reported lengths of one inch (25 mm) were achieved in five weeks, and 2.6 inches (67 mm) were reached in 16 weeks. Additional growth at 0.85 mm/wk (Berrigan 1987; Ingle and Dawson 1952) was expected to produce well shaped marketable oysters (75 mm) in 16 months and superior quality oysters (75–85 mm) in 18-20 months.

Growth rates for surviving stocks were estimated from length frequency distributions. The mean length of oysters on Cat Point was 61.1 mm on 3 October, 72.2 mm on 6 January (0.85 mm/wk), and 82.8 on 29 April (0.71 mm/wk). Because harvesting was prohibited during this period, these data provided the best growth estimates available under relatively natural growing conditions. Juveniles growing at calculated rates were predicted to reach harvestable size in early 1987.

TABLE 3.

Length (mm) of newly recruited oyster stocks by percentile groups from Cat Point and East Hole following Hurricane Elena.

Date	Weeks From Set	1 Percent (mm)	25 Percent (mm)	50 Percent (mm)	Mean (mm)
Cat Point Field Surveys					
1/7/86	13		33	27	32.9
3/12/86	21	50	34	29	32.6
4/29/86	28	69	45	37	40.6
7/31/86	40	80	59	49	52.8
9/22/86	52	89	69	58	58.0
East Hole Field Surveys					
7/86	13	60	28	22	26.7
9/86	52	120	77	56	60.7
1/7/86	62	130	79	66	65.5

Post-Storm Production

Estimated production levels developed from field surveys were used to determine when and where standing stocks would be sufficient to support commercial harvesting (250 bags/acre). Standing stock estimates after the storm indicated that growth and recruitment to marketable size of surviving oysters was substantial. Production estimates for Cat Point improved progressively through the winter and spring of 1985/86; percentage of legal size oysters increased from 22% to 76%; and estimated production exceeded 260 bags/acre by May 1986 (Table 2). Potential production levels from Cat Point were estimated at 260,000 bags.

Several assumptions were incorporated to develop a management plan to permit harvesting. Using a conservative estimate based on 25% harvesting efficiency, approximately 65,000 bags would be available for harvesting.

Since there was no accurate method for determining the size of the fishing fleet following the closure, 200 vessels were assumed as the maximum. Numbers of harvesting days and bag limits were established based on these values. Accordingly, it was assumed that 200 vessels (vessel-trips) could harvest 15 bags/day for 20 days without depleting the resource. Results from field surveys and checkpoint reports demonstrated that available resources were sufficient to support continued harvesting, and the season was extended until 30 June 1986.

Emergency measures were enacted restricting harvesting to levels providing production revenues while insuring against resource depletion. Rules were promulgated specifying areas of the Apalachicola Bay System (St. George Sound, Apalachicola Bay, St. Vincent Sound and Indian Lagoon) where oyster harvesting was permitted four days each week (Monday-Thursday), limiting harvests to a maximum of 15 bags (10 gallons dry measure/bag) per person or vessel per day, limiting harvesting times to sunrise until 4 pm, and requiring that harvesters pass through checkpoints before landing their catch. Other provisions addressed labeling requirements, culling practices, and tolerance limits. These rules also gave the Executive Director of the Department of Natural Resources the authority to further restrict harvesting if stocks were threatened by overexploitation. Additionally, rules designated areas where shellfish resources were severely damaged as Special Resource Recovery Areas.

Reported landings from 5 May through 30 June 1986, demonstrated that estimates of standing stocks were reliable indicators of potential production. Reported landings from checkpoints and length frequency distributions also indicated that stocks were not severely depleted during this period. Landings and catch per vessel did not decline markedly; 39,292 bags of oysters were harvested by 5,023 vessel-trips during 33 days of restricted harvesting (Table 4). Weekly landings indicated that bags/vessels declined from 8.6 to 7.0 over the harvesting period; monthly landings reflected a more moderate decline from 8.3 to 7.4 bags/vessel. The number of vessels engaged in the fishery remained relatively constant; monthly data indicated 152 vessels/day passed through checkpoints. Approximately 65% of reported landings were from Cat Point, 25% from Apalachicola Bay and eastern St. Vincent Sound, and less than 10% from western St. Vincent Sound.

Summer harvesting areas were opened to restricted harvesting on 1 July and remained open through 30 September 1986. Summer harvesting was restricted to the same conditions regulating the Winter harvesting season. During the Summer harvesting season, 40,133 bags of oysters were landed by 5,920 vessel-trips during 53 days (Table 4). Landings declined from 26,592 bags in July to 3,753 bags in September. Results from field surveys on East Lumps, in the Summer harvesting area, indicated estimated production levels had decreased from 427 bags/acre to 168 bags/acre over the season. Sharp declines in estimated production were attributed to limited harvesting areas which were rapidly exploited when harvesting pressure became concentrated.

TABLE 4.

Reported landings from checkpoints in Apalachicola Bay from May 1986–June 1987.

Date	Days	Vessels	Bags	Bags/Vessel
		Winter Harvesting Season 1986		
5/86	16	2,432	20,229	8.3
6/86	17	2,591	19,063	7.4
Total	33	5,023	39,292	7.8
		Summer Harvesting Season 1986		
7/86	19	3,305	26,592	8.0
8/86	16	1,767	9,788	5.5
9/86	18	848	3,753	4.4
Total	53	5,920	40,133	6.8
		Winter Harvesting Season 1987		
10/86	18	2,958	23,358	7.9
11/86	16	3,472	34,370	9.9
12/86	17	3,905	45,459	11.6
1/87	15	5,011	59,766	11.9
2/87	14	5,115	60,088	11.7
3/87	16	5,625	65,982	11.7
4/87	20	9,672	114,464	11.8
5/87	21	8,817	95,185	10.8
6/87	19	5,733	46,359	8.1
Total	156	50,308	545,031	10.8

On 1 October 1986 designated Winter harvesting areas were reopened under constraints regulating continued restricted harvesting practices. Checkpoint reports reflected the predicted low production period at the beginning of the season. Moderate increases in production throughout the fall were attributed to recruitment into legal size classes (75 mm). By March 1987, increased landings were strongly influenced by increased harvesting pressure. Vessels engaged in oyster harvesting and bags landed increased during each successive month through April (Table 4). Highest monthly totals were recorded in April 1987; Landings declined during May and June. Reduced production was attributed to a combination of over harvesting and a seasonal response to warmer water temperatures when metabolic activities are redirected from growth toward reproduction

A total of 545,031 bags were harvested by 50,308 vessel-trips during 156 harvesting days. An average of 10.8 bags/vessel were landed each trip. Harvesting pressure was concentrated in St. George Sound where greater than 78% of the vessels engaged in oyster harvesting accounted for more than 82% of the landings (Table 5). Checkpoint reports indicated that 233,926 bags were harvested from Cat Point and 211,136 bags were harvested from East Hole.

Harvests exceeding 12 bags/vessel indicated that restricted harvesting practices effectively controlled harvesting pressure in St. George Sound (Table 5). Consistently high landings (bags/vessel) also showed that har-

TABLE 5.

Reported landings (bags) from checkpoints during 1986–87 Winter harvesting season in the Apalachicola Bay system.

Date	Days	Vessels	Bags	Bags/Ves.	Ves./Day
			St. George Sound		
10/86	18	1,838	14,984	8.2	102
11/86	16	2,325	24,908	10.7	145
12/86	17	2,848	35,547	12.5	168
1/87	15	3,864	48,227	12.5	258
2/87	14	3,904	48,021	12.3	279
3/87	16	4,777	58,660	12.3	299
4/87	20	8,200	101,072	12.3	410
5/87	21	7,508	83,969	11.2	358
6/87	19	4,085	33,745	8.3	215
Total	156	39,349	449,133	11.4	252
Percent		78.2	82.4		
			Apalachicola Bay		
10/86	18	901	7,191	8.0	50
11/86	16	1,019	8,797	8.6	64
12/86	17	911	8,893	9.8	54
1/87	15	956	9,914	10.4	64
2/87	14	1,017	10,329	10.2	73
3/87	16	700	5,812	8.3	44
4/87	20	1,211	11,136	9.2	61
5/87	21	1,113	9,863	8.9	53
6/87	19	1,488	11,567	7.8	78
Total	156	9,316	83,502	9.0	60
Percent		18.5	15.3		
			Thirteen Mile		
10/86	18	219	1,183	5.4	12
11/86	16	128	665	5.2	8
12/86	17	146	1,019	7.0	9
1/87	15	191	1,625	8.5	13
2/87	14	194	1,738	9.0	14
3/87	16	148	1,510	10.2	9
4/87	20	261	2,256	8.6	13
5/87	21	196	1,350	6.9	9
6/87	19	160	1,047	6.5	8
Tota	156	1,643	12,393	7.5	11
Percent		3.3	2.3		
			Totals		
10/86	18	2,958	23,358	7.9	164
11/86	16	3,472	34,370	9.9	217
12/86	17	3,905	45,459	11.6	230
1/87	15	5,011	59,766	11.9	334
2/87	14	5,115	60,088	11.7	365
3/87	16	5,625	65,982	11.7	352
4/87	20	9,672	114,464	11.8	484
5/87	21	8,817	95,185	10.8	420
6/87	19	5,733	46,359	8.1	302
Total	156	50,308	545,031	10.8	322

vesters in St. George Sound were able to readily take bag limits (15 bags). Harvesters operating in Apalachicola Bay and St. Vincent Sound were less successful harvesting bag limits.

Special Resource Recovery Areas in Winter harvesting areas remained closed to shellfish harvesting at the beginning of the 1986/87 Winter harvesting season. Field surveys from East Hole and Platform Bar Recovery Areas indicated that oyster stocks were insufficient to sustain commercial harvesting. The East Hole Special Resource Recovery Area was opened on 17 December 1986, after subsequent field surveys determined that stocks would sustain harvesting. Harvesting prohibitions on East Hole accomplished several objectives; including protecting sublegal stocks until they reached harvestable size, supplying a needed boost to production at a time when other reefs were becoming depleted, and displacing harvesting pressure from Cat Point.

Monthly landings ranged from 3,753 bags in September 1986 to 114,464 bags in April 1987. Landings from Winter harvesting areas ranged from 19,063 bags in June 1986 to 114,464 bags in April 1987. Landings for Summer and Winter harvesting areas totaled 624,456 bags harvested by 61,251 vessel-trips during 242 harvesting days. Daily averages showed 253 vessels harvested 2,580 bags/day over this period, yielding an average of 10.2 bags/vessel/day.

Resource Restoration

Following Hurricane Elena, efforts were initiated to restore oyster reefs and mitigate economic impacts. Funds allocated for resource rehabilitation from legislative appropriations were used to employ oystermen to transport and transplant live oysters and processed oyster shell. The Department had been actively engaged in collecting oyster shells from processing plants and constructing oyster reefs as part of its Oyster Culture Program. The direction of this program was modified to promote participation by oystermen and cooperation between the Department and the oyster industry. Goals of the restructured program were twofold: to ameliorate short-term economical impacts upon shellfishing dependent individuals and communities, and restore shellfish reefs for long-term benefit of the resource. A total of $443,248 were disbursed among program participants. During this program, 589,613 bushels of oyster shell and 22,180 bushels of live oysters were planted on sites throughout the Bay. Live oysters were relaid from Restricted areas and seed oysters were transplanted from rapidly recovering reefs.

Additionally, the Department requested emergency assistance though the Commercial Fisheries Research and Development Act, Public Law 88-309(4b) to restore severely damaged and depleted oyster reefs. In 1985, $1,570,000 were released from congressional appropriations to restore shellfish resources in impacted areas. During 1986, $918,000 were used to restore 225 acres of severely damaged reefs with 56,470 cubic yards of clam shell, *Rangia* sp. An additional $553,960 were released to complete restoration in Spring 1987; approximately 150 acres were restored using 39,760 cubic yards of clam shell.

Clam shells, dredged from Lake Pontchartrain in Louisiana, were transported by barge to the planting site where they were washed overboard using a high pressure water

stream. Shell was dispersed across reef surfaces at a rate of approximately 250 cubic yards/acre. This practice has proven to be an effective method for establishing suitable bottom for larval oyster attachment. Reefs restored during this program were protected as part of Special Resource Recovery Areas and special management was applied while recovery progressed. Restored reefs are expected to produce marketable oysters as early as two years after planting.

Post-Storm Assessment Following Hurricane Kate

In late November, 1985 severe environmental conditions associated with the passage of Hurricane Kate were again anticipated to adversely effect oyster reefs in Apalachicola Bay. Resource assessments and field surveys of reefs following Hurricane Kate indicated limited adverse impact to reefs or productivity. Damage was observed on reefs where sand was again deposited over productive areas. Field surveys indicated losses of legal and sublegal oyster size classes was minimal, a critical factor which could have influenced recovery. Furthermore, there was no evidence of scour, sediment deposition, or disruption of reef ecology. The presence of attached algae, commensal organisms, and live oysters, including fragile spat, indicated turbulence during Hurricane Kate on most reefs was considerably less than encountered during Hurricane Elena. Abnormally high tides during the most severe periods of Hurricane Kate's passage may have protected reefs from extreme turbulence. In contrast, abnormally low tides were implicated as amplifying the effect of turbulence during Hurricane Elena.

DISCUSSION

Resource Recovery

Resource assessment indicated that the economic stability of oyster dependent industries could not be anticipated based on the condition of oyster resources after the passage of Hurricane Elena. Economic losses suffered by the industry could not be recovered by existing management practices. The short-tem survival of the industry was dependent upon a management initiative to protect the existing resource, promote recovery, and mitigate economic hardship. An emergency rule closing waters of Franklin County to oyster harvesting provided the opportunity to develop a comprehensive management plan. Judicious management required promoting resource recovery while permitting harvesting as soon as the resource was economically viable.

Resource management changes after Hurricane Elena included:

1. altering management plans for Summer and Winter harvesting areas and seasons,
2. changing lawful harvesting times from sunrise to sunset seven days each week, to sunrise to 4 pm Monday through Thursday,
3. changing harvesting limits from 'no limit' to 15 bags per vessel, and
4. restricting culling practices and tolerances limits for undersize oysters to protect juvenile stocks. Management practices for harvesting methods (hand tongs, diving, and wading) and size limits (three inches) remained in force.

Additionally, checkpoints were implemented to monitor harvesting and ensure compliance with resource protection rules.

Notwithstanding regulatory policies restricting harvesting, the immediate future of the resource was dependent on natural recovery resulting from successful recruitment. The rate of natural recovery was also dependent on the degree of structural damage to reefs and timely spatfall.

The most destructive activity, in terms of natural recovery, occurred when live oysters and shell were swept off reefs and deposited in soft sediments or deep troughs. Progressive recovery of reefs sustaining extensive loss of cultch was expected to be slow and largely dependent upon artificial restoration. Reef surfaces covered with sand were also slow to recover, while areas devoid of sand improved rapidly. Early in the recovery process, abrasive activity of shifting sand limited survival of fragile spat and eventual reestablishment of sand covered reefs. These reefs may not return to full productive potential for many years and may require extensive reconstructive efforts.

Erosion of compacted layers of sediments and shell rubble obliterating reef surfaces was critical to natural recovery. On Cat Point, surface erosion eventually exposed underlying reef components, including live oysters and shell. Within two weeks, reefs covered by fine shell improved substantially compared to those portions of East Hole and Platform Bar covered by sand. It became evident that when structural components were not destroyed, rapid natural recovery followed. Management practices were developed to protect surviving stocks and promote recovery dependent upon extent of damage and prospect for natural recovery of individual reefs.

Successful spatfall and subsequent survival are critical factors controlling natural recovery processes. Since seasonal spawning activity for oysters in Apalachicola Bay may continue into November (Ingle and Dawson 1953), protecting the surviving population was expected to enhance natural population renewal. Fortuitously, environmental conditions remained favorable and high levels of spat settlement were reported by 2 October 1985. Substrate conditions on many reefs were optimal for larval attachment and survival. Cultch was well scoured of fouling organisms such as barnacles, mussels, and algae. Erosion of fine sediments from reef surfaces continued to expose ideal surfaces for larval attachment weeks after the storm.

Juvenile recruitment following the storm was readily differentiated from surviving stocks. This obvious separation of populations provided an ideal natural laboratory to

investigate growth rates. Earliest recruited juveniles were monitored until they reached harvestable size and surviving oysters were monitored throughout the period they were protected. Table 3 shows growth among percentile groups which were closely associated with the fastest growing oysters (1%), the first identifiable peak (25%), and the mode (50%), as represented in length frequency distributions. Although conditions following Hurricane Elena were atypical for Apalachicola Bay, results from field surveys contributed to our understanding of growth under natural conditions.

Oyster length frequency distributions for Cat Point indicated a bimodal population distribution when recent recruitment was described separately from surviving populations. Comparisons between populations indicated a paucity of subadult oysters (45–65 mm) suggesting that storm related losses among juveniles was extensive. This bimodal distribution pattern suggested that a period of low productivity was inevitable between the time when surviving stocks were harvested and recently settled juveniles reached harvestable size. Juveniles were not expected to reach legal size before 1987, indicating production shortfalls at the beginning of the 1986/87 Winter harvesting season.

Determining the most advantageous time to begin harvesting was complicated by the threat of mortality among harvestable stocks. A degree of risk is involved in allowing harvestable stocks to remain on the reefs, as potentially high rates of mortality may occur among large oysters during the summer months (Quick and Mackin 1971). Evaluation of these and other issues indicated that carefully regulated harvesting would be the most judicious management practice. Restricted harvesting would act to mitigate short-term economic constraints without impeding resource recovery.

To comply with this plan, restricted harvesting was permitted in specific Winter harvesting areas. Harvesting was initiated in May and continued through June, when the Summer harvesting season began (1 July 1986). The Summer harvesting season was altered to exclude July and include September; previously July was included in the Summer harvesting season and September in the Winter Harvesting Season. The 1986/87 Winter harvesting season was delayed until 1 October to comply with production estimates.

It was unclear at the beginning of the Winter harvesting season whether newly recruited stocks would ameliorate predicted production shortfalls. Oyster abundance was obvious, but their quality and marketability were uncertain. Oysters exhibiting rapid growth (75 mm/yr) were typically elongate, resulting from intensive setting and crowded conditions. Rapid shell growth was characterized by shallow valve contours and thin shells. They are locally called "coon oysters" or "scissor bills" and were often found in dense clusters. Oysters broken away from clusters during harvesting and culling often demonstrated greater shell growth in other dimensions and were typical of more desirable "cup oysters".

However, strong market demand was the dominant factor governing sales and values. Although product quality was considered inferior to products before the storm, dockside value was higher when Winter harvesting resumed in 1986. Assuming a conservative dockside value of $10 per bag, 1986–87 Winter season landings would be valued at $5.45 million; at dockside values of $12 per bag, landings would be valued at $6.54 million. These estimates suggested that, not only was recovery successful, but that 1987 may have produced the highest annual value recorded for oyster resources from Apalachicola Bay.

Enactment of emergency policies to regulate resource recovery in Apalachicola Bay following Hurricane Elena demonstrated that debilitated shellfish resources could be successfully managed. These actions produced the most judicious use of impaired resources, promoted resource recovery, and insured long-term resource conservation. Management practices also confirmed the necessity for and reliability of comprehensive planning based on resource assessment and fishery statistics. Additionally, cooperation between federal and state agencies produced numerous successful programs which sustained the shellfish dependent industry and economy through depressed periods. Most importantly, these policies and programs combined with the recuperative capacity of Apalachicola Bay and its dynamic resources, produced the resurgence of a prosperous industry.

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THE CONSEQUENCE OF BAYMEN: THE HARD CLAM (*MERCENARIA MERCENARIA* LINNÉ) MANAGMENT SITUATION IN GREAT SOUTH BAY, NEW YORK

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ABSTRACT The hard clam (*Mercenaria mercenaria* Linné) supports a significant shellfishery in New York. Almost since the inception of the fishery in the mid-nineteenth century, considerable effort and expenditures of public funds have been made to manage the shellfish resource and the industry. However, landings have fluctuated dramatically. While many factors are responsible for this, baymen (watermen) are an integral part of the management framework and are, therefore, in a position to determine the success of the management effort, yet their role is rarely considered. A case history analysis of the Great South Bay, New York hard clam fishery is presented to examine the consequences of baymen in hard clam management and, in particular, how baymen have blocked technically valid management proposals from possible implementation. This, in turn, is used to suggest ways in which shellfish management can be improved.

KEY WORDS: baymen, shellfish management

INTRODUCTION

New York has consistently been a leading producer of the hard clam or quohaug (*Mercenaria mercenaria* Linné) in the United States. In 1986, approximately 104,000 bushels, valued at $3.8 million were harvested from New York's marine waters (New York State Department of Environmental Conservation, unpublished). The commercial fishery has its origins in the mid-nineteenth century (Ingersoll 1887) and by 1891, hard clam landings had reached 565,000 bushels (Smith 1894). Almost since the inception of the fishery, considerable effort has been expended to protect and promote the shellfish industry, primarily by seeking to maintain and enhance hard clam abundance and, hence, landings. To this end, various town, county, and state agencies have adopted regulations, undertaken studies, and initiated various stock improvement programs. These management efforts have entailed the sizeable expenditure of public funds. However, hard clam landings over the past century have not been stable, experiencing three periods of expansion followed by dramatic declines.

Many factors, both human and natural, have contributed to the fluctuations in harvest. Beginning in the early 20th century, closure of shellfishing areas to harvesting due to pollution has caused many locally important shellfisheries to collapse and approximately 17% of New York's marine waters are presently closed (New York State Department of Environmental Conservation, unpublished). Prior to the Second World War, hard clams were of secondary interest and importance relative to oysters and, therefore, attracted less consistent fishing and management effort. It is also likely that natural variability in hard clam abundance played a role in the fluctuations.

Management may have dampened these factors, but it may also have had little, none, or even a negative effect. With the considerable historic effort to protect the shellfishery, it is reasonable to ask if the management has been optimal or if there is some aspect of the management effort that has inhibited its effectiveness.

An effective management program is contingent upon an adequate scientific or technical basis and the implementation of the requisite actions (Pringle 1985). In theory, technical merit should be the primary factor determining a course of action, yet technical merit does not always ensure implementation of effective measures or prevent the adoption of ineffectual actions. Social and political considerations are often of equal, if not greater, importance in determining management initiatives (Kennedy and Breisch 1983).

Baymen (watermen) who harvest hard clams from New York's coastal waters have historically been active in shellfish management and an important political constituency. Their ability to influence management goals, priorities, and the implementation of management initiatives has certainly contributed to the effectiveness of the hard clam management effort. In spite of their importance, the consequences of the baymen in the shellfish management effort are rarely considered. This paper examines the role baymen have played in establishing the management regime using a case history analysis of the hard clam fishery in Great South Bay, a shallow embayment on the south shore of Long Island, New York, where shellfishing has been a traditional occupation for over 150 years, as an example. The analysis focuses on the baymen's role in the management process, on the way that management reflects their attitudes, and on the possible impairment of the management effort.

THE GREAT SOUTH BAY SHELLFISHERY

The Great South Bay is one of several hard clam producing areas in New York. It is a shallow bar-built bay on Long Island's south shore (Figure 1), is approximately 50

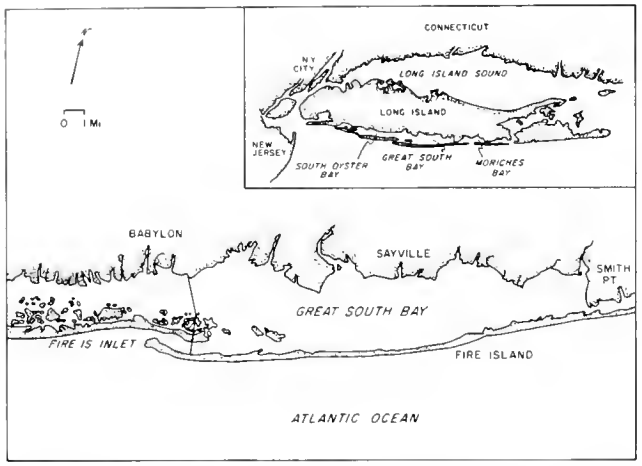

Figure 1. Location of the Great South Bay, New York. The Bay's shellfishery was originally based on the oyster (*Crassostrea virginica*) but because of environmental changes over the past three decades, oysters have become extinct and the fishery is totally dependent upon the hard clam (*Mercenaria mercenaria*).

km long with widths up to 8 km. It has an area of approximately 1.6×10^5 hectares.

Only residents of three of Long Island's thirteen townships - Babylon, Islip, and Brookhaven - can legally harvest shellfish from the Great South Bay because of local residency restrictions. Beginning in 1970 the number of baymen harvesting hard clams can be approximated from the sale of commercial shellfishing permits by the New York State Department of Environmental Conservation to residents of these towns (Table 1). The number of permits is only a fair estimate of effort as no distinction is made between part-time and full-time shellfish harvesters.

Great South Bay hard clam landings are available since 1945 and are given for the years 1960 to 1986 in Table 2. Landings began to rise in the early 1960s due to increased hard clam abundance and increased fishing effort (COSMA 1985). Between 1963 and 1971 landings quadrupled and the number of baymen probably doubled (Town of Brookhaven unpublished). According to Buckner (1983), by 1974 the catch-per-unit-effort had begun to decline, indicating the resource was being overfished. The number of baymen and landings, however, continued to increase until 1976.

Beginning in 1977, landings and commercial shellfishing permits began to fall due to a decline in hard clam abundance (Buckner 1983). By 1980, both landings and permits had dropped by over half. The rate of decline slowed by mid-decade and by 1986 baymen were reporting increased individual catches (K. Guyer, President, Brookhaven Baymen's Association, pers. comm.).

Hard clams are harvested from small (10 m) boats by baymen individually or, rarely, in pairs (Figure 2). Hard clams are harvested year round and only hand-operated gear, rakes or tongs, are permitted; most baymen harvest hard clams exclusively. A bayman's hard clam catch and, hence, gross income, is dependent upon endurance and skill, as well as the abundance of hard clams.

TABLE 1.

The number of shellfish harvester permits sold by the New York State Department of Environmental Conservation to residents of the Townships of Babylon, Islip, and Brookhaven (New York State Department of Environmental Conservation, unpublished). The number of permits is the only estimate of the number of baymen working on the Great South Bay and includes both full-time and part-time harvesters.

Year	Permits	Year	Permits
1970	3,863	1978	4,913
1971	4,517	1979	4,608
1972	4,534	1980	4,275
1973	4,796	1981	3,998
1974	5,788	1982	3,145
1975	6,149	1983	2,355
1976	6,517	1984	1,926
1977	6,694	1985	1,406
		1986	1,282

Several aspects of the hard clam shellfishery have facilitated involvement in management to a greater degree than in other fisheries and baymen have a long tradition of involvement in shellfish management (Taylor 1983). Shellfish management is a largely local initiative by virtue of Colonial patents to the Townships of Babylon, Islip, and Brookhaven, which have given them ownership of the bay bottom and therein the shellfish resources. Town records, for example, the Trustees' Record of the Town of Brookhaven, contain numerous references to requests and petitions for town intervention to improve the shellfish resource or to enact legislation to assist the industry. Baymen also return to port each day and shellfishing is concentrated in several communities along the length of the bay, both providing baymen access to the management process. New York State's management role is primarily regulatory on matters of statewide concern and on public health issues.

TABLE 2.

Bushels of hard clams landed from the Great South Bay from 1960 to 1986 (New York State Department of Environmental Conservation, unpublished).

Year	Bushels	Year	Bushels	Year	Bushels
1960	147,268	1970	565,600	1980	338,389
1961	130,734	1971	611,553	1981	309,140
1962	137,045	1972	620,817	1982	201,654
1963	154,386	1973	571,324	1983	178,422
1964	251,052	1974	616,431	1984	146,792
1965	343,184	1975	653,058	1985	117,341
1966	385,413	1976	700,465	1986	104,296
1967	513,266	1977	658,443		
1968	461,403	1978	547,773		
1969	523,319	1979	422,946		

Figure 2. Harvesting hard clams from the Great South Bay. Both rakes and tongs are used.

Other government agencies, most notably Suffolk County, fund research, undertake management planning studies, and provide economic assistance to baymen.

The involvement of baymen in management has also been institutionalized to a certain extent by government, particularly at the town level. Baymen have considerable political influence and shellfish management is oftentimes a political issue (COSMA 1985). Before the creation of town management departments in the mid-1970s, elected town officials at times were apparently guided by the assumption that the baymen knew what was best for the shellfish industry and acquiesced to baymen's requests. The towns often delegated management responsibility to the baymen by having baymen undertake the projects funded by the towns. Even after management departments were created, baymen's access and involvement in decision making was preserved by "shellfish advisory commissions" established to offer guidance and advice to their respective towns.

Baymen's attitudes toward management have not been reported in any detail. The baymen are probably similar to other fishermen in that they see harvesting hard clams as a way of life and not just a job (Townsend 1985). Based on various public statements (for example, Losee 1985; Freedman and Morris 1983), the following composite profile emerges. Baymen see themselves as independents pitted against government and seek limited interference. They support efforts to enhance hard clam abundance through planting seed (sub-legal) hard clams or spawner clam (broodstock) transplants but generally oppose regulations that would limit fishing effort or alter the way the fishery operates. Baymen vociferously oppose leasing of bay bottom for private mariculture. Baymen have different priorities than managers, holding that the objective of management should be to help make a "day's pay" while managers focus on the resource.

CASE HISTORY ANALYSIS

There are fundamentally two ways to sustain the shellfish harvest and avoid a boom-bust cycle. Either more hard clams can be put into the bay to keep pace with the unregulated harvest—for example, by releasing hatchery raised sub-legal size seed hard clams and decreasing natural mortality through predator removal—or, the rate of removal can be regulated at a level which will support sustained yields. These are not mutually exclusive initiatives as enhancement can be used to rebuild stocks and sustain higher levels of effort. Without harvesting controls, however, enhancement can turn into just providing hard clams for more baymen with no individual baymen benefitting from the management effort.

The need to control harvest effort has long been recognized (COSMA 1985). The use of more efficient mechanical gear has been prohibited since the mid-19th century when the uncontrolled use of dredges caused resource depletion. A minimum size limit was temporarily instituted in the 1890s and has been permanent since 1942. The residency restrictions in effect provide limited *de facto* entry control. There have been periodic mentions of the need to further limit effort, but it wasn't until 1985 that even a freeze in the number of baymen was formally proposed (COSMA 1985). It did not receive popular support and no other controls have been implemented.

Most of the management effort has been directed at increasing the hard clam abundance in the Great South Bay and enhancement programs enjoy considerable support (COSMA 1985). The planting of spawner clams has been undertaken almost continuously since the 1930s and over 2,000 bushels are presently planted annually. The planting of hatchery raised seed hard clams has been practiced since 1975 on varying scales. Transplanting hard clams from closed shellfishing areas to open areas where they can be harvested after 21 days of depuration has been periodically undertaken since the late 1930s.

Management efforts were intensified in the mid-1970s as the shellfish industry was expanding. Each of the towns created full-time management programs. In addition to town enhancement programs, Federal, State, and local funding was made available for basic scientific research to gain a better understanding of the Great South Bay, the factors affecting hard clam abundance and the enhancement of hard clam abundance (Wise 1985). However, measures to control fishing effort received little attention.

A wide variety of options are avilable that have the potential to maintain the productivity of the shellfish industry (Suffolk County Planning Department 1987). In the case of the Great South Bay, stock enhancement dominates the management philosophy. There are many reasons why

some management options are chosen over others. Two options that are technically valid, but have not been implemented, are limiting effort and private leasing. Two of the findings of the Coastal Ocean Science and Management Alternatives (COSMA) Programs's assessment of the hard clam industry are relevant (COSMA 1985):

- "Present regulations on hard clam harvesting have not restricted the total harvest to a level the resource can support."
- "Private mariculture is not a management alternative for rehabilitating and sustaining the wild harvest, but may play an important role in the future of hard clam production and in the preservation of the traditional lifestyle of baymen."

Whether the prior institution of the implied limited effort program or the private mariculture program would have prevented the collapse of the hard clam industry can only be speculated upon. Both could have made important contributions to the management effort. For example, in the soft clam fishery in Maine, restricted access areas had a 15% greater yield than unrestricted areas (Townsend 1986). In Virginia's portion of the Chesapeake Bay, the oyster harvest has been increased substantially by combining a public fishery with private culture (Kennedy and Breisch 1983).

Neither limited effort nor private mariculture are new concepts and were available in the mid-1970s. Baymen today oppose these concepts even after the drop in landings and number of baymen, when both should be much more attractive than they would be during rising or stable harvests. It is, therefore, unlikely that neither limited effort nor private mariculture could have been established during the peak years of the shellfish industry.

The recommendation for entry freeze in the COSMA (1985) report did generate considerable debate (Freedman 1985). Baymen response was largely negative and most were skeptical of the concept, although a general dissatisfaction with shellfish management may have contributed to baymen opposition (O'Malley 1985). There was virtually no public support and no follow-up discussion to the proposal at any level.

The lack of action on the limited entry proposal is due in large part because there was little public support from the baymen (Morris 1987). In the past, other unpopular management proposals and actions resulted in legislative intervention (see, for example, Smith 1982) so that shellfish managers and researchers would have little incentive to propose a program which would be doomed from the outset. Elected officials would not be expected to further a proposal that lacked popular support.

Baymen in New York have opposed private mariculture for a variety of reasons (Kassner 1988). In 1984, the New York State Urban Development Corporation proposed a private mariculture program targeted to assist baymen. Low interest loans and underwater land were to be made available to baymen to undertake small mariculture projects to demonstrate mariculture as an alternative source of income. Baymen opposition to the leasing component was a factor in the program being abandoned (N. Rosan, N.Y. Urban Development Corporation, pers. comm.).

That baymen support enhancement and reject limiting effort and private mariculture is consistent with baymen's attitudes. Enhancement makes the resource appear to be unlimited and does not disrupt their way of life. In addition, with all the emphasis on enhancement, there may be little perceived need to limit effort. Limiting effort means more government interference and control, while leasing takes away traditional freedom of access. The baymen have political power, allowing them to set the management agenda, so that the emphasis on enhancement is not surprising.

TOWARD IMPROVED MANAGEMENT

It is tempting to blame the baymen for the failure of the management effort because they have blocked technically valid management initiatives from consideration. This, however, is an oversimplification. Baymen are simply acting in a way that they feel will protect their beliefs and livelihood. If there is to be a change, it is incumbent, therefore, upon those managing the resource and industry to address both the concerns of the baymen and the protection of the resource.

Successful management first requires establishment of goals. No management objectives have been established for the Great South Bay hard clam fishery. Management, in general, has tended to be *ad hoc* and driven largely by sociological and political considerations. It must be clear to baymen, shellfish managers, and elected officials why and for what purpose the fishery is being managed. Failure to do so will almost certainly lead to controversy. Without goals, it is impossible to evaluate the success or failure of management initiatives.

Once the goals have been established, there are two ways they can be achieved. The necessary management actions could be imposed unilaterally or government and baymen could develop a cooperative partnership, recognizing that management must achieve both technical and societal goals. There is precedence for acting arbitrarily, but the action and the initiative would almost certainly be controversial. Baymen would probably rationalize violating the initiative if they felt it was unjust (McCay 1984), thereby increasing enforcement costs and risking management anarchy.

It is probably much more beneficial to all concerned to cooperate on management even if the final initiative is somewhat less efficient than it might have been had it been imposed unilaterally and without compromise. Maximizing biological or economic efficiency may, in fact, not be desirable. For example, Smith (1980) suggests that reducing landing variability may be better for the fishermen than

managing for maximum sustainable yield and still conserve the resource. Less than optimally efficient regulations may still be beneficial if they are less socially disruptive (Townsend 1985). Management that enjoys popular support will tend to be much more effective in the long term.

When management initiatives have been proposed, shellfish managers tend to expect that baymen will respond rationally and altruistically. However, people do not always act rationally in the collective and are influenced by such things as past experience, inadequate communication, interpretational biases, and insufficient information (Miller 1983). When baymen do not respond favorably to what managers see as good science, it can generate animosity even if the baymen are acting rationally from their perspective. Managers all too often fail to take into consideration the baymen's needs and point of view.

Shellfish managers also must recognize that there have been management failures in the past. Part of the baymen's distrust of management is founded in past events and collectively baymen have a good long term memory (McCay 1984). For example, there were abuses in leasing Great South Bay when it was practiced extensively during the late nineteenth century and it is this issue that is raised in some form whenever leasing is brought up. Building confidence is a long process.

The way in which management initiatives are presented is also critical and in the case of the limited entry and private mariculture proposals, could have been a factor in the baymen opposition. The initiatives were presented more as concepts than as plans of action with detailed descriptions and analyses. Fishermen, in general, are more concerned about personal impacts than promise (Townsend 1985). Without the details of either program, there was no way for the baymen to assess the consequences to them, as baymen, so that they were almost obligated to protest these initiatives even though they could have been supportive. For example, baymen as a group are seen as opposing limited entry and private mariculture, yet an anonymous survey of baymen showed them to be supportive of both programs (Town of Brookhaven unpublished).

Successful management will require the integration of baymen's needs with accepted management concepts. It will require greater trust and cooperation among legislators, managers and baymen. The baymen must recognize the technical requirements of successful management and managers must be sensitive to the social impact of management actions. It is clear that all parties have contributed to the collapse of the hard clam fishery and only through concerted effort will the fishery be restored and maintained.

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SHELLFISH AQUACULTURE AS A COTTAGE INDUSTRY: A MODEL FOR DEVELOPMENT IN NEW YORK

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ABSTRACT Employment in small-scale, labor intensive marine aquaculture—a local cottage industry—is in many ways comparable to that in commercial catch fisheries. It can be undertaken by individuals with limited financial resources and hence limited risk. It can be restricted to small plots for independent, individual users. If successful, it can supplement commercial fishermen's incomes which are as highly variable as landings and market prices. To preserve their independent lifestyle in the face of competition over marine resources, baymen may have to consider small-scale aquaculture production as a means of insuring the existence of commercial harvests. The promotion of aquaculture as a cottage industry in New York may break the socio-economic impasse which has stifled development of this industry to date.

KEYWORDS: shellfish aquaculture, Long Island, industry development

INTRODUCTION

New York state's marine coastlines are nearly all found on Long Island; a discussion of shellfish aquaculture in New York, therefore, is a discussion of the development of this industry on Long Island (see Figure 1). In contrast with the freshwater aquaculture industry of "upstate" or inland New York which is a much larger and more diverse enterprise (New York State Aquaculture Association Newsletter, June, 1988), marine aquaculture in New York continues to develop slowly in the face of a number of technical, economic and social obstacles. The purpose of this paper is twofold: first, to outline the development of Long Island's marine aquaculture industry to date by illustrating several of these key obstacles to industrial development; and second, to propose a model for continued development of marine aquaculture, principally of molluscan shellfish, which may be most appropriate given the obstacles which have impeded the development of shellfish aquaculture on Long Island.

Before entering into a discussion of the historical opportunities and constraints to aquaculture development on Long Island, it is worthwhile to consider the distinction between public and private aquaculture, two approaches which are particularly important on Long Island.

In broad terms, public aquaculture programs use public funds provided through government agencies to increase harvestable stocks to aquatic resources for the benefit of the public, including the fishing industry. Public aquaculture generally means programs to enhance important commercial and recreational fisheries. In practice, harvestable stocks enhanced by public aquaculture programs have been available to all members of the public whose taxes and fees underwrote the program. This implies that at some point in the organism's life cycle, public aquaculture programs must distribute the cultured stocks to the public, or make them accessible, and thereby relinquish control over the fate of the "crop." The benefits of public aquaculture are obvious when stocks are made available to the public at harvestable sizes (*e.g.*, freshwater lakes stocked with cultured finfish for "fee fishing"), however for molluscan shellfisheries, the benefits of public aquaculture are equivocal.

Public shellfish aquaculture programs are run on limited budgets; they can buy or produce a relatively large number of very small, hence inexpensive, bivalve seed stock or a smaller number of larger, more expensive, seed stock. Because there is considerable local support from commercial shellfishermen (termed "baymen" on Long Island) for highly visible seed planting programs which release as many seed clams as possible (see Kassner, 1988; see also reports of the Leasing Subcommittee of the New York State Shellfish Advisory Committee, referenced in Committee minutes, March, 1988) public shellfish aquaculture tends to plant as large a number as possible of very small seed stock onto public grounds. On these areas of public bay bottom, the seed face several season's additional growth before reaching legal harvest size. After such planting, very little is, or can be, done to assure the growth and survival of this publicly-owned crop. Unfortunately, the smaller the size of seed planted, the lower the survival to harvest (see Flagg and Malouf, 1983). Public aquaculture of molluscan shellfish is highly intensive (in hatcheries, land-based and field nursery systems) up to the point of seed planting at which time it ceases to be aquaculture at all. This "abandonment" at release is an important feature of public aquaculture on Long Island: at the time of planting, neither commercial nor recreational shellfishermen have derived any benefit from the efforts of the public aquaculture program, and any benefits of such an abbreviated form of aquaculture depend on the survival and growth of seed stock in the uncontrolled, poorly understood and often highly variable natural environment.

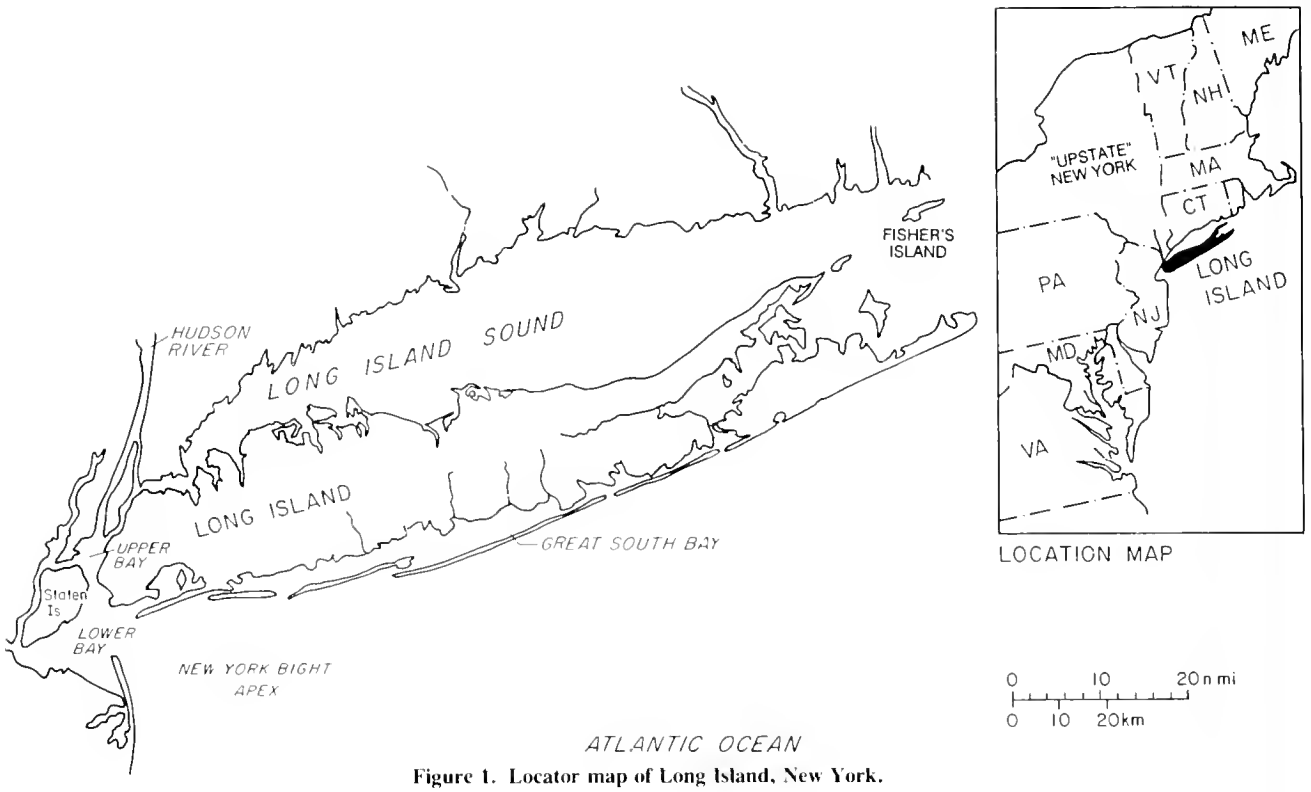

Figure 1. Locator map of Long Island, New York.

On the other hand, private aquaculture uses private funds and resources to maintain as much control over the crop as economically feasible until such time as the greatest economic benefits may be derived from the sale of products, either as seed stock or marketable shellfish. The benefits of private aquaculture, usually cash revenues, accrue solely to the individuals or corporations whose resources were used to generate the revenues. The private aquaculturist has made a more significant, personal investment of time and money in a crop than the taxpayers or baymen who have relatively minor, personal investments in the publicly produced shellfish.

Finally, there are several important relationships between public and private aquaculture programs on Long Island, summarized in Figure 2. Most public aquaculture programs acquire shellfish seed stock from private aquaculture facilities on Long Island or out-of-state. Private aquaculturists derive substantial economic benefits from sales of seed (see Malinowski, 1986), and are able to diversify sources of revenue while sustaining cash flow required for continued development of methods to culture shellfish to marketable size. Public aquaculture programs often rely on the expertise of private aquaculturists in resolving technical problems of production (some towns now produce their own seed) and planting. Finally, many private aquaculturists are dependent upon state, county or town agencies to permit exclusive use of areas of bay bottom for grow-out of seed stock to marketable size. Thus, the public agencies regulate the space required by the aquaculturist while the private aquaculturist produces seed stock and can provide technical assistance for public seed planting programs.

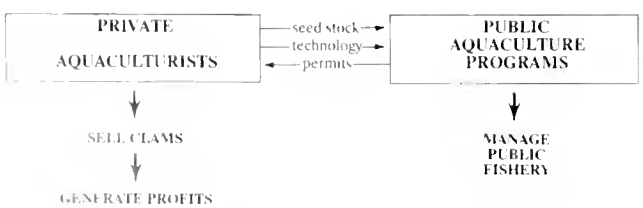

Figure 2. Relationships between private and public aquaculture.

Davies (1982, 1984) reviewed the aspects of Long Island which favor aquaculture development. He noted that nutrients and temperature regimes are particularly favorable for the reproduction, growth and survial of several commercially important shellfish species. Private shellfish aquaculture on Long Island has been successful for several species including the eastern oyster, *Crassostrea virginica* and the hard clam, *Mercenaria mercenaria*. Long Island communities rely heavily on marine-related economic activities, and maritime expertise is abundant. Baymen generally support government-sponsored public aquaculture programs, and in some cases, government-sponsored private shellfish transplanting activities which may benefit the public fishery. Davies also noted the proximity of Long Island to very large marketing channels (in New York City and on Long Island) for high quality seafood.

Indeed, there have been substantial economic activities related directly or indirectly to private aquaculture on Long Island for many decades. Some of the pioneer studies of molluscan hatchery methods were conducted at Long Island

institutions by Wells and Glancy in the first half of this century (Wells, 1933; Glancy, 1965). The privately-held firm of F. M. Flower and Sons of Oyster Bay, Long Island, which has been culturing and harvesting oysters since 1887 (and additionally hard clams since 1984), is one of the preeminent examples of successful shellfish aquaculture in the nation. And the Blue Points Company, of West Sayville, Long Island, which produced oysters during its early years (from 1888 to the mid-1950's) and now harvests both cultured and naturally produced hard clams, is one of the largest private shellfish aquaculture firms in the nation with more than 13,000 acres of bay bottom owned on the basis of a 300 year old "patent" (land grant).

One might ask, then, why private shellfish aquaculture on Long Island remains an emerging industry. Why aren't there more than an handful of private shellfish culturists on Long Island? What are the important constraints to further development of the industry?

Davies (1982) and Siddall and Davies (1985) reviewed several problem areas for continued aquaculture development on Long Island. Constraints include a lack of action by either state, county or town agencies to implement mechanisms which encourage, or even make possible, expanded private aquaculture activity. It is commonly assumed that these governmental positions are maintained by legislators and politically-appointed agency leaders who are sensitive to the opinions of well-organized and traditional marine user groups, in particular Long Island's commercial shellfishermen. While local definitions of "traditional" often fluctuate over time (*e.g.*, shellfish relaying programs are the traditional activity in Delaware Bay; L. Taylor, personal communication), Long Island's definition of traditional shellfisheries has not changed for decades. Suggestions of change for Long Island's traditional, independent catch shellfisheries seem to be taken even by the public as an attack on the fundamental traditions of the Island.

Throughout 1986 and 1987, a series of public meetings were held to solicit input from a wide range of marine interest groups on the preparation of a planning document (Koppelman and Davies, 1987). This public process confirmed the widely held perception that commercial shellfishermen of Long Island publicly oppose the exclusive use of bay bottom (required for private shellfish aquaculture) on the basis that successful culture of shellfish on privately controlled underwater lands may lead to expanded or consolidated private aquaculture ventures which might eventually exclude independent shellfishermen from Long Island's productive shellfishing grounds and result in inappropriate market competition. Trends in many U.S. industries substantiate the baymen's concerns; very few small firms which have achieved success remain small, but rather expand and gain a larger market share, in this case, at the expense of independent baymen. One of the few successful shellfish culture companies on Long Island actually has demonstrated something similar to this phenomenon, over the course of several decades, by buying out the leases of several marginal shellfish producers in a town-managed bay. Clearly, the baymen's concerns are well founded.

Additionally, and perhaps more importantly, many full-time commercial shellfishermen on Long Island are decendants of baymen who fought in Long Island's legendary "Oyster Wars" of the 1890's (see Taylor, 1983, for an ethnohistory of this community and this conflict between large companies and independent operators over access to shellfishing beds and markets). Therefore, many of the spokespeople of the baymen's organizations on Long Island draw on a personal, family history of opposition to the sort of exclusive use of large tracts of underwater lands which they perceive to be an outcome of continued aquaculture development (see also Matthiesen, 1986, for an informal, non-fictional account of the plight of baymen on Long Island).

Other important constraints to aquaculture development exist as well. There is no secure, long-term access to small tracts of bay-bottom for use in private aquaculture. The state Department of Environmental Conservation, which has responsibility (under section 13-0301 of the state Environmental Conservation Law) for much of the state-owned underwater lands of Long Island (excluding the most productive areas controlled by counties and towns), implemented a program which has issued only eight 2 hectare "Temporary Marine Land Use Assignments" for aquaculture purposes, three of which ceased activity soon after issuance as a result of private, developmental obstacles. The state has not leased any other underwater lands for shellfish culture in recent history and those areas which remain under private control from "franchises" granted earlier in this century are too expensive for use by small-scale aquaculture developers. Financing for aquaculture enterprises is as difficult on Long Island as it is in many other parts of the nation, but the very high cost of energy, labor and supplies on Long Island amplifies funding difficulties. Finally, there are a number of ambiguities in state, county and town laws which affect the management of marine resources. On the basis that their charters predate the U.S. Constitution, some of the towns in eastern Long Island manage and allocate marine resources under their jurisdiction in contradiction to state law, and while such "home rule" may present an opportunity to local aquaculture interests, potential investors cannot be confident that state or county regulations will favor aquaculture investments. Contrasts between local, regional, state and national policies on aquaculture development are being investigated by Davies (doctoral dissertation at the Marine Sciences Research Center under the supervision of Robert Malouf).

COTTAGE INDUSTRY MARINE AQUACULTURE

Many of the constraints to marine aquaculture development on Long Island are summarized diagrammatically in Figure 3 which depicts the situation as an impasse.

There are a number of technical (biological) obstacles to aquaculture production of marketable shellfish. While

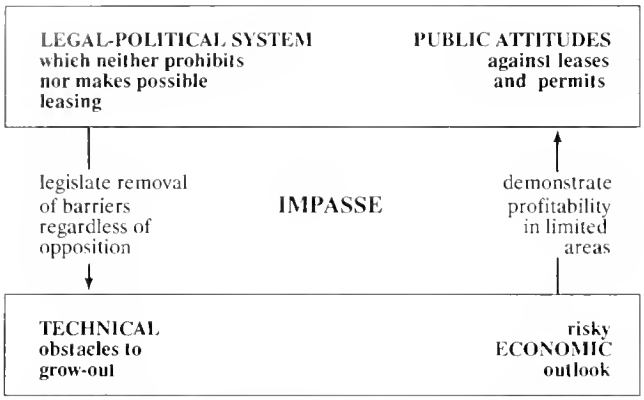

Figure 3. Summary of relationships among technical, economic, social and legal forces which maintain the impasse to private shellfish aquaculture development on Long Island.

many production problems in the hatchery have been resolved, and land-based and field-based nursery techniques have been refined (*e.g.*, Koppelman, 1984; Manzi, *et al.*, 1984; Malinowski and Siddall, in press), grow-out of seed stock to market size has proven to be a formidable obstacle to economic success (*e.g.*, Flagg and Malouf, 1983). The economic outlook for shellfish aquaculture on Long Island hinges primarily on improvements in culture methods which increase survival from seed to market size. Economic viability is not likely to be demonstrated until someone having exclusive access to bay-bottom resolves these technical barriers and makes money raising shellfish. Until then, private shellfish aquaculture remains a risky enterprise. Very few investors are willing to take financial risks required to develop this new industry, especially in the face of widespread, vocal opposition to leases and exclusive access to underwater lands. At the same time, opposition is unlikely to moderate in favor of an economically unproven activity. The result is an impasse to development. Without access to resources, there is minimal development of improved methods. Without improvements in methods, investment remains risky. Without a basis for profitable investment, there is little pressure to open access to private aquaculture.

Figure 3 also presents two (of many) approaches which might be used to break this impasse in favor of aquaculture development. The first, presented on the left side of the figure, is titled "legislate removal of barriers regardless of opposition." Within this approach might be listed a number of recommendations which have been made in the past, including the designation of a lead state agency for aquaculture development and the convening of a conference of involved state, county and local agencies to implement a regulatory program involving the granting of leases (the legal questions in this instance would be monumental). This approach assumes that legislators would be willing to bear the consequences of baymen's opposition to aquaculture development, which seems unlikely given the perceived electoral power of this vocal marine interest group. This approach also assumes that it is possible to coordinate regulatory authority and management among a broad range of state, county and local governmental units.

The alternate approach, presented on the right side of Figure 3 and titled "demonstrate profitability in limited areas," is the basis of the cottage industry model for marine aquaculture development. The state Department of Environmental Conservation, in implementing temporary assignments for access to limited areas of bay bottom, has initiated this alternate approach however the program has important restrictions. Assignments and renewals may be made unless substantive and non-mitigable objections are brought forward during a public review process. Aquaculturists may culture shellfish on floating structures, bottom racks, *etc.*, if other required permits can be obtained, but they may not free-plant seed stock onto natural substrates on the assigned bay bottom. The purpose is to insure that the shellfish inventory can be removed in case conditions on the assigned bay bottom become inappropriate for assignment, that is, if natural shellfish populations develop on the assignment. In this instance, renewal of the assignment may not be possible because the state is not empowered to lease or assign any underwater lands which are naturally productive of shellfish.

Important examples of successful, small-scale aquaculture operations are The Clam Farm and Ocean Pond, of Fisher's Island, New York (see Figure 1). The Clam Farm, a private aquaculture facility in operation since 1982, operates on a two hectare temporary assignment, sells shellfish seed stock to several town programs and is involved in several development programs aimed at improving the grow-out process for several bivalve species. The lack of a local molluscan shellfishery on Fisher's Island is one of the principal reasons why there continues to be minimal opposition to The Clam Farm. Clearly, this is not the case on Long Island proper, but recall that the basis for most opposition to private aquaculture development is the perception that the industry would eventually acquire a substantial fraction of Long Island's underwater lands which have production potential for shellfish. The location of the Island further offshore than most of Long Island results in lower mean water temperatures, a shorter growing season, and hence affects some shellfish culture practices (see Malinowski, 1986), however, aquaculture facilities in the Island's near-shore waters have been productive. The stated goal of this family-operated company is to provide an annual income to the owner/operator and seasonal employment to one or two part-time employees. The details of The Clam Farm operation, which emphasizes manual labor and minimal technology, are reported in Malinowski (1986). A central theme of this practical manual is the similarity between the daily work routines of small-scale, private aquaculturists and independent catch shellfishermen.

The continuing experience of The Clam Farm suggests

that one to two people working a two hectare temporary assignment are likely to be able to secure financial returns which are similar to those of full-time, commercial shellfishermen on Long Island (see Malinowski, 1986). A simple calculation of the percentage of the bay bottom of Long Island required to support all current full-time shellfishermen (licensed through the state) is revealing. There are nearly 65,000 hectares of coastal waterbodies on Long Island which are open to shellfishing by fewer than 500 baymen who earn a substantial part of their total income from shellfishing, and another 2,000 for which shellfishing provides supplemental income (New York State Department of Environmental Conservation data, 1988). Even if all full-time shellfishermen shifted from catch fisheries to private aquaculture each on a two hectare temporary assignment, more than 98% of Long Island's shellfishing grounds would remain in the public domain. These calculations are not meant to suggest that all shellfishermen should examine aquaculture as a substitute for traditional shellfisheries, nor do these simplistic estimates account for the competition between catch fisheries and aquaculture for potentially productive shellfishing grounds (note that areas which are naturally productive of shellfish cannot be leased under current state law). The figures do suggest that small-scale, private, shellfish aquaculture leases, controlled by individuals for individual income, could exist without having a substantial impact on the total acreage available to catch shellfisheries. If such small assignments of bay bottom (not productive of natural shellfish at the time of leasing) were granted on a renewable basis with 10–20 year terms, and could be held only by private individuals and never aggregated into larger holdings, then many of the substantive, non-biological obstacles to private shellfish aquaculture on Long Island might be resolved.

Minor legislative revisions to state, county and town laws, regulations and policies could make possible the development of a cottage industry in shellfish aquaculture, however they are unlikely to be implemented without some support from commercial shellfishermen. In fact, several amendments to state laws (Shellfish Advisory Committee, 1988) and a state-sanctioned aquaculture council (almost exclusively focussed on freshwater aquaculture, however) have been proposed. Identifying the legal mechanisms to promote shellfish aquaculture is not the obstacle; convincing shellfishermen to support any level of aquaculture development is the principal challenge. Obviously, the constituencies of the shellfishermen's associations will have to demonstrate to their elected leadership new interests in shellfish aquaculture if their organizations are to alter their official policies which oppose exclusive allocation of marine resources to private aquaculture.

One goal of public aquaculture programs is to dampen fluctuations in natural abundances and stabilize landings. Small-scale, private aquaculture may be viewed as an additional means to reduce the individual's dependence on highly variable natural stocks and hence stabilize personal income. As shellfish abundance varies in some waterbodies (*e.g.*, the 75% decline in hard clam landings in the Great South Bay, Long Island, between 1977–1987), full-time baymen are obliged to increase fishing effort to maintain personal income. Small-scale, private aquaculture production could supplement income from marginal catch fisheries. Shellfishermen may have to become more involved in aquaculture or aquaculture-like processes which assure themselves of consistent, commercial harvests.

More than one public institution has attempted to promote further consideration of shellfish aquaculture on Long Island. Through support for the publication of a clam culture manual (Malinowski, 1986) specifically oriented to the baymen, much as is Castagna and Kraeuter's (1981) manual, the New York State Urban Development Corporation attempted to generate interest in shellfish aquaculture in the community of Long Island baymen. Additionally, the Cornell Cooperative Extension—Suffolk County (New York) Marine Program has organized several day-long workshops to introduce the opportunities and constraints of marine aquaculture to the public, including commercial fishermen. In fact, of all the marine interest groups, the commercial shellfishermen appear to be the most qualified to undertake the sort of low- to no-technology, labor-intensive shellfish culture which is the basis of a cottage industry approach.

The most compelling arguments for the participation of shellfishermen in private aquaculture development may come from changes in the environment rather than from promotion by public institutions. For example, recent losses in Long Island's fisheries have led to closer cooperation between commercial shellfishermen and private aquaculturists. Extraordinary, coastal phytoplankton blooms during 1985–1987 (Cosper, *et al.*, 1987; Nelson and Siddall, 1988) nearly eliminated bay scallop populations which once were the basis for a commercial fishery in New York. Efforts to replenish natural populations were based on the importation of bay scallop seed stock produced by private aquaculturists both within and outside of the state. Several "spawner sanctuaries" were established in the area (Siddall, *et al.* 1986) under the management of baymen's associations. Members of the associations husbanded the seed stock to insure the success of the replenishment effort, and with technical advice from private aquaculturists, became temporary practitioners of a public version of the enterprise so many had opposed in its private form.

Reduced bacteriological water quality and closure of shellfishing grounds will exacerbate these trends of variable landings and market price. Long Island is already a densely populated area; according to census data, if Long Island were a state, it would be more populous than 25 of the 50 United States. Additionally, population surveys indicate that within 20 years, nearly all towns on Long Island will be at or very near saturation densities (LIRPB, 1984); the

associated shifts in land use will almost certainly be accompanied by increased point and non-point sources of pollution. Public perception of this problem (*e.g.*, cover stories of "Troubled Waters," BusinessWeek October 12, 1987; "Our Filthy Seas," Time, August 1, 1988) is mounting, and if ex-vessel prices for naturally-produced shellfish fall as a result, baymen may have to increase harvests in order to maintain levels of personal income. The higher yields per unit area which may eventually be possible through aquaculture production represent an alternative means of sustaining shellfishing as an important economic activity on Long Island.

Based on national shellfish water quality indicators, approximately 18% of all of New York's marine habitats (most, such as Long Island Sound, not amenable to shellfishing) are uncertified (falling below national water quality standards for shellfish harvesting). When new indicators of contamination for purposes of certifying shellfish growing waters are redefined (Kilgen, 1988) and applied in the mid-1990's, it is almost certain that there will be major shifts in the areas open for commercial and recreational shellfishing. It is not clear if changes in water quality standards will increase or decrease the acreage available to shellfishermen, however several programs which transplant naturally-produced shellfish from uncertified to open waters are likely to be curtailed by a redefinition of the indicators of shellfish growing water quality. In the face of greater restrictions on areas for shellfish harvest, private, small-scale aquaculture may become an economically important means of producing shellfish on Long Island.

Finally, aquaculture products have several advantages in the marketplace which may become more important as federal seafood inspections are mandated. According to William Stelle (U.S. Senate Subcommittee on Fishery and Wildlife Conservation and the Environment; personal communication), several U.S. congressional initiatives (HR1483, HR3735 and S1813) requiring continuous inspections of all seafood (and poultry) products are very likely to be passed and implemented within "the next two to three years." Cultured seafood products are likely to be easier and cheaper to inspect, and may be held for optimum market prices, then sold with a more positive image based on the fact they are farmed rather than caught from wild stocks.

CONCLUSIONS

The opposition of Long Island's commercial shellfishermen to private aquaculture has inhibited the development of this potentially important industry for many decades. Marine aquaculture, particularly molluscan shellfish aquaculture, is an industry in conflict with the traditional lifestyle of the region's baymen. Private aquaculture is not "institutionalized" and has few vocal supporters; if the *status quo* is maintained, opportunities for private aquaculture on Long Island may soon disappear. If revenues from traditional shellfisheries decline, both forms of shellfish production may be given very low priority when marine resources are reallocated as population densities on the Island increase.

Changes in the coastal environment, and new regulatory policies to deal with them, may substantially enhance the opportunity and need for small-scale, marine aquaculture in the area. The careful promotion of a cottage industry in marine aquaculture may prove to be the only model acceptable to influential commercial shellfishermen who may have to consider small-scale aquaculture as a supplement to income from their independent lifestyle on the water.

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THE LOUISIANA OYSTER FISHERY: INDUSTRY AND MANAGEMENT CONFRONT A CHANGING ENVIRONMENT

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ABSTRACT Rapid changes in Louisiana's coastal environment have greatly afftected the distribution of the state's estuarine and estuarine dependent fisheries resources. The American Oyster, *Crassostrea virginica*, has been one of the most severely impacted species due to its' relatively stringent habitat requirements. Increasing salinities have shifted oyster production away from the historic reefs at the seaward fringe of the estuarine basins and toward the central and upper portions where substrate is generally limiting. The oyster industry has responded to the shifting zone of productivity by leasing additional waterbottoms in areas that are currently or potentially productive. In those areas where substrate is limiting, oyster farmers often "create" reefs by depositing cultch material. The controlling state agency, the Louisiana Department of Wildlife and Fisheries, has reacted to the changing conditions in a number of ways: expanding and intensively managing the public oyster grounds; implementing a cultch planting program on the public grounds; operating existing freshwater diversion structures for salinity control; and cooperating in the design and construction of larger and more efficient freshwater diversions.

KEY WORDS: oyster fishery, management, changing environment

INTRODUCTION

Oyster (*Crassostrea virginica*) (Gmelin) production in Louisiana over the past several years has averaged over 12 million pounds annually with a dockside value of approximately 22 million dollars. Louisiana production generally ranks first among the Gulf States and first or second nationally. The 1985 landings of 14.2 million pounds was valued at nearly 24 million dollars dockside (Table 1). The Louisiana oyster industry is labor intensive and, as such, is a large employer within the coastal community. In addition, this industry has an importance to Louisiana's culture and heritage commensurate with its considerable economic impact.

In contrast to the other major oyster producing states, Louisiana has basically maintained a consistent harvest throughout this century. Environmental degradation is most often blamed in those states where oyster production has decreased. Louisiana, however, has not been immune to changes within its coastal environment. In fact, the state's coastal wetlands are being lost at a rate of 50 square miles per year. This land loss has had a dramatic effect on the distribution and quality of certain aquatic habitats, including those suitable for oyster production. This paper examines: the development and organization of Louisiana's oyster industry; the changing environment within which the industry must operate; and the various efforts of management and industry, both existing and proposed, to deal with the changes.

DEVELOPMENT AND ORGANIZATION OF THE INDUSTRY

Coastal Louisiana is characterized by extensive estuarine areas created over the past 5,000 years by the deltaic processes of the Mississippi River. Oyster populations have flourished and declined in the vicinity of each of the emerging and retreating delta lobes. While oysters have undoubtedly been exploited in this region since prehistoric times, the first commercial operations took place in the early 1800's in the estuaries near the present Mississippi River Delta. In the mid-1800's, immigrant fishermen from Dalmatia realized that high quality oysters could be produced by transferring small "seed" oysters from the natural reefs near the delta to bedding grounds closer to the Gulf of Mexico. These higher salinity areas did not support substantial natural populations due to the inability of recently set oysters to survive the high predation, but were excellent for fattening and growth of transplanted seed. Increased demand in the later 1800's for these superior, transplanted oysters prompted the fishermen to recommend state legislation which was both supportive of their method of cultivation and protective of the natural reefs as a source of seed.

By the turn of the century, the state's oyster producing areas had been divided into public seed grounds and private bedding grounds (Figure 1). The public grounds included the most productive natural reef areas east of the Mississippi River. Much of the remainder of the oyster producing areas were made available for private leasing. Leasing pro-

TABLE 1.

Louisiana Oyster Landings and Dockside Value 1981–1986

Year	Landings (Millions of Pounds)	Value (Millions of Dollars)
1981	9.0	16.2
1982	12.0	17.0
1983	13.3	17.6
1984	14.0	25.3
1985	14.2	23.8
1986	13.8	22.4

Source: Louisiana Landings—National Marine Fisheries Service.

cedures were placed under the jurisdiction of the Oyster Commission of Louisiana. Additionally, the Commission was made responsible for supplying a source of seed oysters from the public grounds.

Thus, the basic organization of the fishery was established. The state supplied the seed, and the private leaseholders would transfer the seed to their leases for growth to market size. The system has endured over the years with the fishermen dredging the public seed grounds each fall, loading their boats with year-old, one to three inch seed, and transporting and bedding the seed on their leases. An individual fisherman may make 20–50 trips per year from the seed grounds to his leases which may be over 50 miles away. The seed usually remains on the leases for six to nine months before harvesting with each boatload of seed returning one to two boatloads of market oysters. If, in a given year, there is an overabundance of seed on the public grounds, market oysters >3 inches are dredged on the grounds the following year, and are either sold directly or used as seed.

In the mid-1900's, the state established four seed oyster reservations, one east and three west of the Mississippi River, to supplement seed production on the public oyster seed grounds. The reservations are opened or closed in response to conditions within the industry, as opposed to the public seed grounds which are opened every year. Additionally, the public grounds were expanded to include Vermillion and Atchafalaya Bays and a tonging reef was established in Calcasieu Lake.

THE CHANGING ENVIRONMENT

In order to understand how Louisiana's rapidly changing coastal environment has affected the state's oyster resources, a basic appreciation is necessary of the geological, hydrological and biological processes involved.

Over the past several thousand years, coastal Louisiana was literally created by the sediment laden waters of the Mississippi River. Periodic floods would spread the river's freshwater and sediment into the coastal areas, rejuvenating existing wetlands and actually building new land in the shallow coastal waters of the Gulf of Mexico. The delta building process would gradually lengthen the main channel's route to the sea. At approximate 500 year intervals, the increasingly inefficent channel would be abandoned in favor of a shorter route where the delta building process would start anew (Coleman and Gagliano 1964).

The abandoned delta, no longer influenced by the river's freshwater and sediment, would deteriorate due to subsidence, erosion and saltwater intrusion, gradually reverting to open water. Historically, the net effect of these deltaic cycles was positive, with the rate of land creation exceeding the rate of deterioration.

Throughout this century, however, man's activities have essentially eliminated the formative deltaic processes of the river while at the same time accelerated the processes of deltaic decline. These activities included the control and containment of the Mississippi River and dredging and channelization in the coastal wetlands.

Together, the natural processes and man's activities are responsible for land loss rates in coastal Louisiana of 50 square miles per year (Gagliano et al. 1981). The loss of land and the reduction in riverine input has had pronounced effects on the hydrology of the estuarine basins.

Land loss has increased wave action, increased the tidal prism, decreased the ability of the estuarine basins to retain freshwater and, in general, increased salinities throughout the estuarine areas. Reduced riverine input has also increased salinities and has limited freshwater input to highly variable local rainfall.

These hydrological changes, in turn, have had equally pronounced effects on the regions estuarine and estuarine dependent fisheries resources. The most important of the hydrological changes, with respect to fisheries, has been increased salinities. Salinity is perhaps the single most important factor influencing the distribution and abundance of estuarine organisms (Gunter et al. 1974). This is particularly true with respect to oysters.

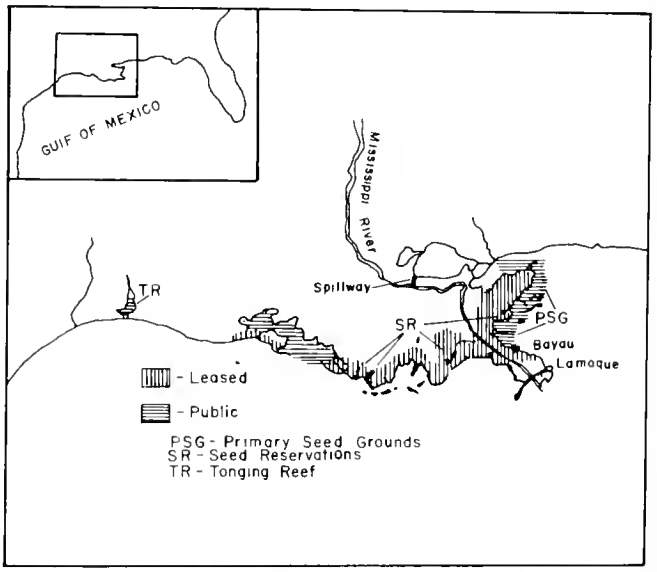

Figure 1. Oyster growing areas of Louisiana.

Oyster populations in Louisiana flourish only within a very narrow range of salinities (Chatry et al. 1983). Salinities less than 10 parts per thousand (ppt) throughout the spring and summer inhibit spawning and reduce larval survival, resulting in insufficient numbers of mature oyster larvae. When salinities greater than 15 ppt predominate, mature larvae are abundant but setting and survival of recently set oysters is poor due to increased numbers of fouling organisms and predators.

Over the past 50-75 years, the historically productive reefs have been rendered non-productive due to increasing salinities. These vast reefs were created over hundreds of years by successive generations of oysters. Salinities favorable for oyster production now occur primarily in those areas which were formerly freshwater habitats.

The "shifting" of the favorable salinities away from the historically productive reefs and toward the headwaters of the estuarine basins has posed serious problems for the oyster industry. Since the transition has taken place over a relatively short period of time, the areas which now have favorable salinities lack extensive reefs for larval settlement. Also, the proximity of the resource to the headwaters of the basins has increased the likelihood of massive freshwater induced oyster mortalities resulting from periodic floods. Finally, the oyster resource is now located closer to areas of human habitation and development, increasing the chances that the sanitary quality of the growing waters may be compromised.

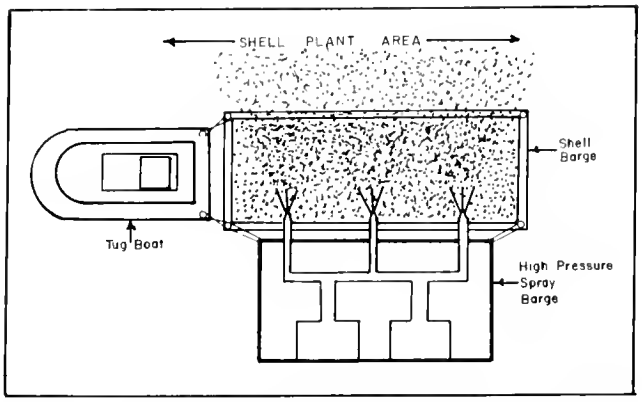

Figure 3. Arrangement of tugboat, shellbarge and spray barge for the planting of cultch material.

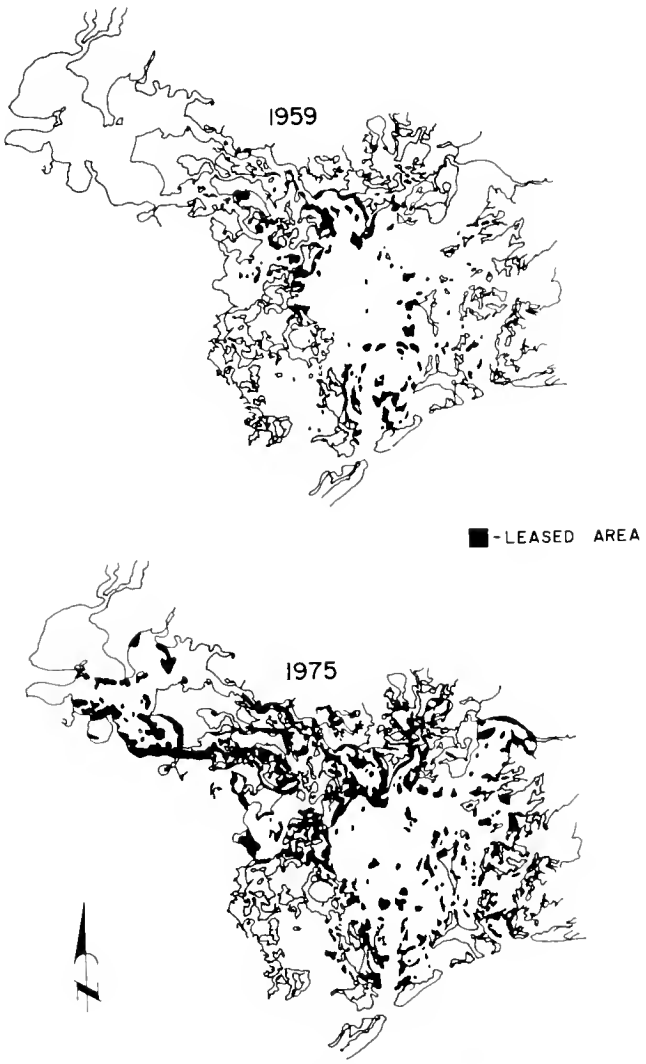

Figure 2. Private oyster leases in the Barataria Bay area in 1959 and in 1975. (From Van Sickle et al. 1976).

INDUSTRY AND MANAGEMENT REACT

Despite the problems associated with increased salinities, Louisiana's oyster harvest has been fairly consistent through the years. Aside from the vastness of Louisiana's estuarine areas, the consistancy of harvest can be attributed to a combination of successful management practices and a willingness on the part of the industry to evolve.

The basic statutory organization of the oyster fishery, as previously mentioned, provides a great deal of flexibility to industry and management. For example, while the law has designated all of Louisiana's oyster growing areas as either public or private, it also allows for the expansion, reduction, and intensive management of each in response to changing conditions.

The public oyster grounds originally consisted of only those natural reef areas east of the Mississippi River. These are referred to as the "Primary Seed Grounds" in Figure 1. In response to increasing salinities and in an attempt to augment the supply of seed oysters, additional public grounds both east and west of the river have been established over the past 40 years. These additional grounds include the four intensively managed seed oyster reservations. The individual reservations are opened or closed depending on the abundance, size and/or condition of the oysters. If, in a given year, there is a shortage of oysters on the public grounds as a whole, then all the reservations may be opened. On the other hand, if oysters are abundant, the reservations may remain closed or be selectively opened for

limited time periods. Additionally, restrictions limiting harvest to "bedding only" or "market production only" are periodically implemented to maximize the available resource. At present, attempts are being made to establish additional reservations in areas where favorable salinity conditions currently exist or are anticipated.

The laws governing the administration of the private grounds are equally flexible and, in fact, encourage private participation. With the exception of the public grounds, practically all existing and potential oyster growing areas in the state are available for private leasing. Oysters may be harvested from the private leases year round. The terms of lease favor the industry. An individual may aquire as many leases as he desires provided the total area leased does not exceed 1000 acres. Leases are granted for a period of 15 years with the leasee given the first right of renewal. The annual rental for oyster leases is two dollars per acre.

These liberal guidelines and reasonable rentals allow speculation on the part of the industry. Fishermen not only lease areas which are currently productive, but they also hold leases in areas which may become productive as salinity conditions change. Figure 2 shows an area of privately leased water bottoms in 1959 and in 1975. The expansion towards the head of the basin is a result of both actual and anticipated increases in salinity.

A problem common to the public and private grounds is the lack of extensive reefs in areas of favorable salinities. In these areas "cultch materials" (clam shells, oyster shells, limestone) must often be deposited to provide suitable substate for larval settlement.

On the public grounds, the state has planted over 1 million yd^3 of cultch material since 1926 (Chatry 1987). While reef oyster shell and steam-plant shell have been used, the preferred cultch material since the mid-1960's has been clamshell (*Rangia cuneata*) (Sowerby). Clamshell is readily available and produces well-shaped oysters that require minimal culling. Clamshell is dredged hydraulically from deposits in certain coastal lakes, loaded onto flush-deck barges, and transported to seed grounds. The shell is planted using a specially designed "spray barge" with a high-pressure water pump and four to six nozzles (Figure 3). Streams of water are directed at the loaded barge and shell is washed overboard in a thin, even layer for a distance of 30–40 ft. from the barge. The speed at which the

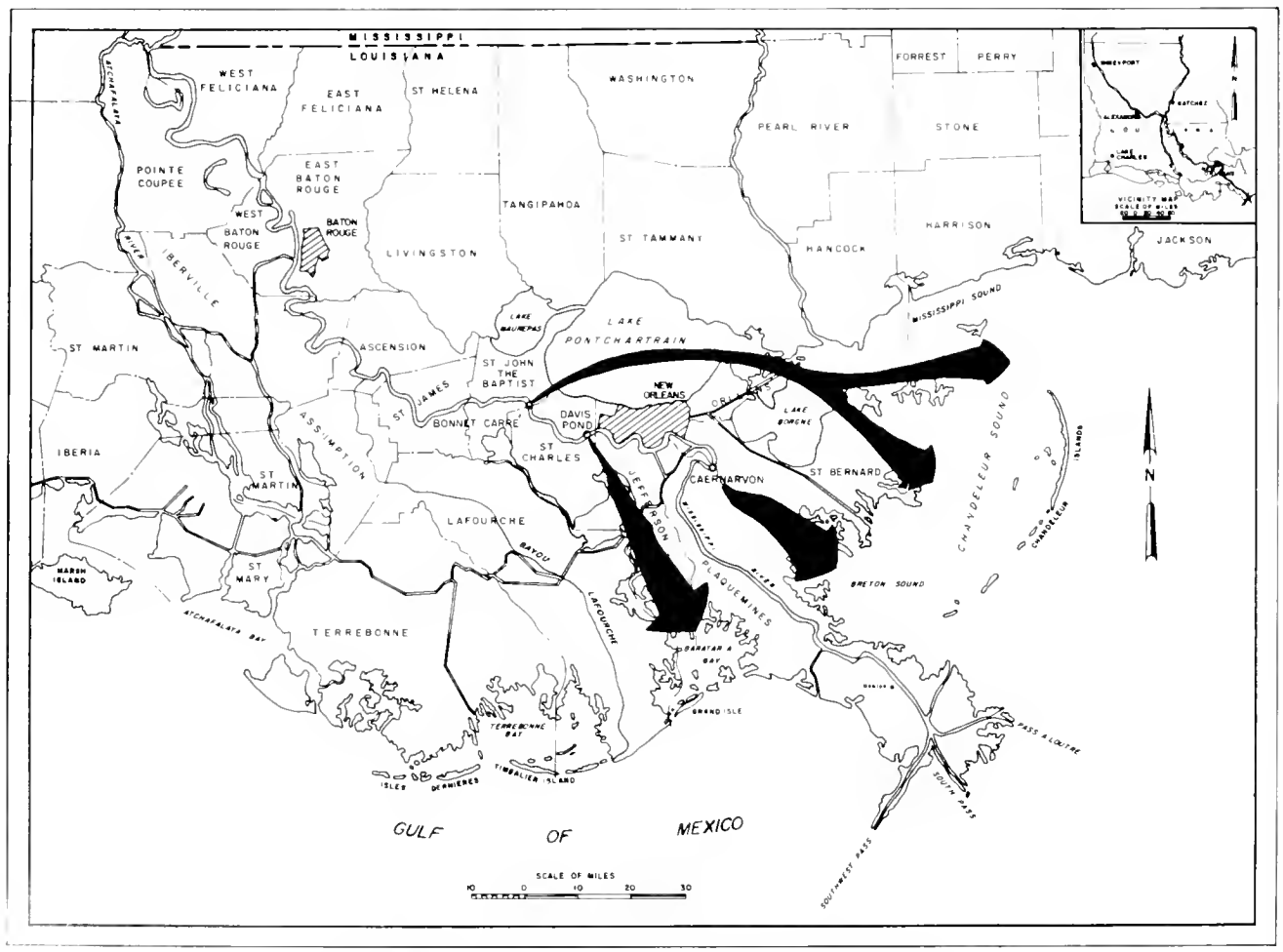

Figure 4. Proposed freshwater diversion sites and areas of influence.

two barges are manuvered determines the planting rate (usually 50–100 yd^3/acre).

On the private grounds, cultch planting is carried out on a much smaller scale, most often by the individual fishermen with his personal vessel. While clamshell is sometimes purchased by the fishermen for planting, an agreement is usually made with a shucking house for discarded oyster shells. The shells are planted on the private leases by shoveling or with assistance from an on-board water pump. Those fishermen who regularly plant cultch material are among the more successful in the industry.

Intensive management and ambitious cultch planting programs, however, have not solved all of the oyster industry's problems. Droughts, periodic floodwaters and inferior sanitary water quality in some growing areas continue to plague the industry. Even more disturbing, these problems will become more severe as the coast deteriorates and salinities increase.

In 1906 the Oyster Commission of Louisiana recommended that freshwater be diverted from the Mississippi River to the oyster growing areas so that "more suitable oyster producing conditions would exist." In 1958 a diversion structure was built to supply freshwater to a portion of the public grounds east of the river. Despite the less than optimal placement of the structure, it has been effective. Today, large-scale controlled diversion projects, now being planned, offer the greatest hope for the continued vitality of Louisiana's estuarine systems and the oyster resource (Figure 4).

Freshwater diversion from the river could reestablish the vast historically productive reefs in the lower portions of the estuarine basins. This would be of considerable benefit to the industry. The present reliance on cultch planting operations would be decreased. The oyster resource would be less susceptible to massive, freshwater-induced mortalities from periodic floods. And, importantly, inferior sanitary water quality would be less of a problem since the resource would be farther removed from areas of human habitation and development.

CONCLUSIONS

Louisiana oysters are an excellent example of the "renewability" of a fisheries resource. After 150 years of exploitation and habitat modification, the industry flourishes. While these past successes may be at least partially attributable to the vastness of the state's estuarine areas, the industry's fate 150 years hence will certainly be determined by the resolve of management and industry.

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LIMITED ENTRY: PANACEA OR PALLIATIVE?
OYSTERMEN, STATE INTERVENTION AND RESOURCE MANAGEMENT IN A DUTCH MARITIME COMMUNITY

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ABSTRACT Shellfishing in the estuaries of the Dutch province of Zeeland is millenia old. Until 1870 these fishing grounds and, concomitantly, shellfish were, in theory at least, common property resources. But the *de facto* rights to the watery commons were sometimes controlled by local fishermen, who regarded the shellfish beds in the neighbourhood of their villages as their territory. In the latter part of the 19th century the natural oyster banks were divided into parcels and leased at public auctions to the highest bidders, who gained exclusive access rights. This state regulation resulted in an increasing capitalization and industrialization as well as in a boom in production. At the same time it favoured social inequality and forced many oystermen out of business. The measure also caused resource management problems, which, paradoxically enough, were due to the initial success of the limited entry legislation. This paper focuses on these and subsequent difficulties in oystering and on the question of how Zeeland oystermen have tried to solve these problems.

KEY WORDS: Zeeland oyster industry, resource management, enclosure of the commons

INTRODUCTION

Resource management problems in fisheries are often attributed to their common property nature. Fishery economists, especially, have pointed out that fishermen who enjoy unrestricted access to fishing grounds seek to maximize their profits in the short run, since fishing is a zero-sum game in which one man's gain is another's loss. In the course of time fish stocks were over-exploited and the fishing industry gradually became overcapitalized through the agency of *Homo economicus* (cf., e.g., Anderson 1976; Gordon 1954; Hardin 1968; Pontecorvo 1967; Pontecorvo and Mesznik 1976; Scott 1955).

In a well-known and oft-quoted paper, the biologist and human ecologist Garrett Hardin points out that "[r]uin is the destination toward which all men rush, each pursuing his own best interest in a society that believes in the freedom of the commons. Freedom in a commons brings ruin to all" (Hardin 1968, p. 1244). In response to this "tragedy of the commons" proposition, many 'fishcrats' and fisheries economists have proposed a number of marine resource management strategies, the most marked ones being limited entry measures and, more specifically, the introduction of property rights over fishing waters. They regard these regulations as a solution, nearly a panacea, which would result in less likelihood of over-exploitation, greater efficiency in the use of capital resources and higher net incomes to fishermen (cf. Anderson 1976, p. 76–77, 82; Gordon 1954, p. 134; Pontecorvo 1976, p. 164–66). By auctioning the rights to the fishery to the highest bidders, as suggested by Anderson (1976, p. 76–77) and Pontecorvo (1967, p. 166), the government would be able to collect the bulk of the revenues.

As a matter of fact, this situation existed in the Dutch oyster industry from 1870 until the First World War and was superseded by similar, albeit more flexible, measures. The purpose of this paper is to evaluate some of the pros and cons of the restricted access legislation mentioned above and subsequent state interventions. The questions underlying it are: What were the consequences of coastal resource management for a) oystering and b) the oystermen? In addition, developments in the Zeeland oyster fishery prior to the introduction of the lease by public auction are described, so as to facilitate comparison between free oyster fishery and mariculture.

Most of the empirical data regarding oyster culture since 1870 will refer to Yerseke, the country's foremost shellfish centre. The town is situated at 51°29′ N and 4°02′ E in the province of Zeeland on the southern bank of the Oosterschelde, a saline inlet penetrating about 48 km inland from the North Sea. It is in the basin of this inlet where most of the oyster plots in The Netherlands are located (see Figure 1). Today Yerseke has a population of 5900, with a large number of residents directly dependent upon shellfish (i.e. mussel, oyster and cockle) farming and shipping or other maritime pursuits, like shrimping and eel fishing. There are two harbours for the local fishing-fleet, which consists of more than a hundred well-equipped boats, ranging in size from 17 to 40 meters. Each vessel is manned by a crew of 2–4 persons.

OYSTERMEN AND COMMON PROPERTY

The earliest evidence of shellfish gathering and fishing in Zeeland dates back to the Mesolithic (5000 B.C.). Archeological excavations in Aardenburg show that mussels and oysters were part of the diet of contemporary coastal dwellers. When the Romans settled this area, they confronted a population which depended largely on agriculture and cattle-breeding for its livelihood, but which supple-

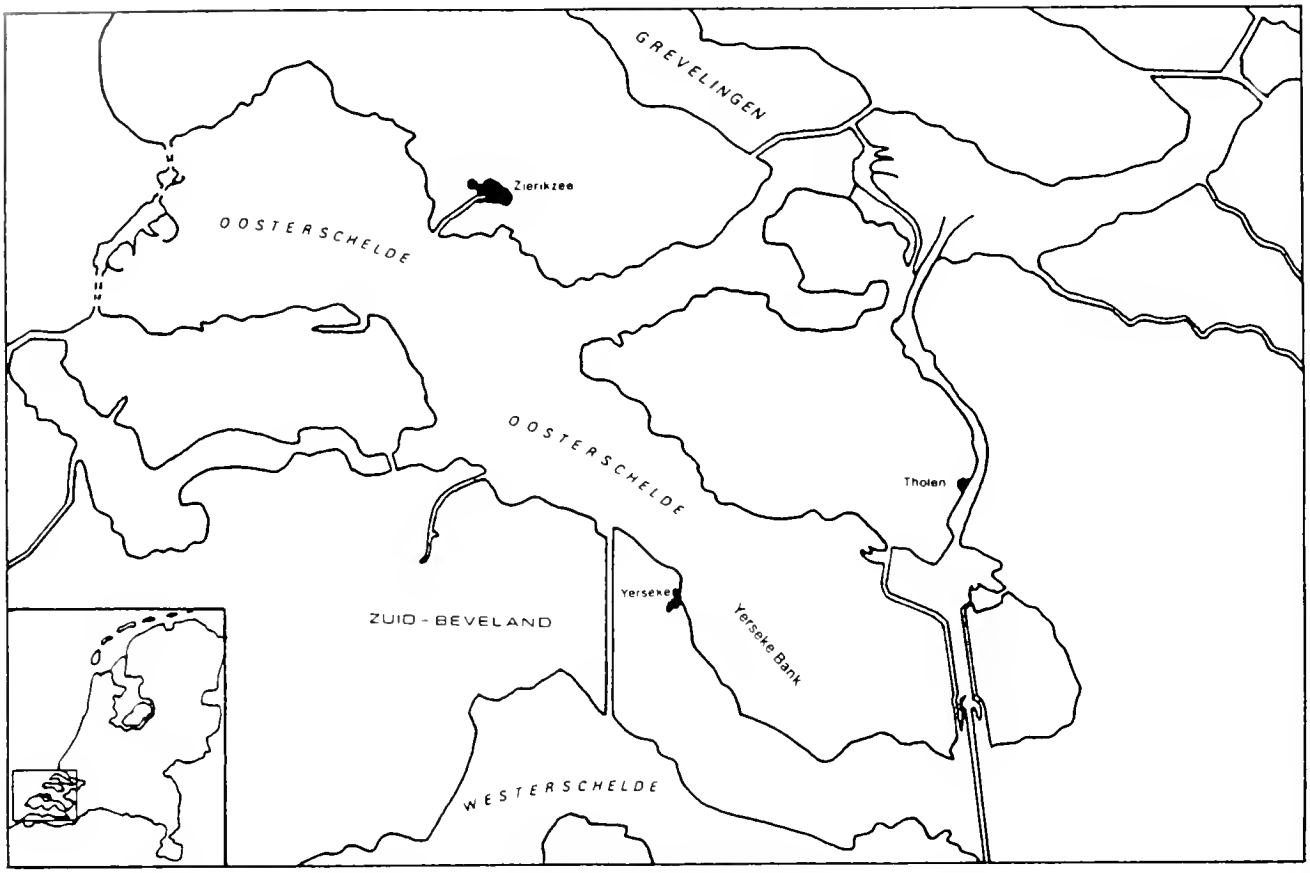

Figure 1. Zeeland streams, 1987.

mented its diet with seafood. Sailing craft were already in use then. From the 3rd until the 9th century habitation of the Zeeland islands was impossible, because of the so-called 'Dunquerque Transgression.' Large areas were inundated during this era. After the 9th century the region was gradually reoccupied and protected from the sea's influence through the building of dikes. In subsequent centuries there has been an ever-growing interest in fishing and shellfishing, not only as a subsistence activity, but also as a commercial venture. Preconditions for this development were population growth, the rise of cities (especially in Flanders) and the establishment of international trade networks.

The Zeeland fishermen diversified their activities, hunting several marine species in different seasons and dredging or gathering shellfish from the tidal flats, according to the tide. They were scarcely able to eke out a scanty livelihood, selling their catch to local merchants who distributed it to customers at home and abroad. The favourable geographical position of Zeeland, with urban centres close at hand, stimulated the evolution of the fisheries to no small extent. In the 15th century the herring fishery flourished, but Zeeland lost its leading position to the province of Holland a century later. Following this decline, more and more fishermen turned to shellfishing. They exploited natural shellfish beds, using flat-bottomed boats, called *hoogaarzen* and *hengsten,* which were particularly well-adapted to sail the shallow estuaries in this region.

Most of these waters were, in theory at least, a common property resource. But the *de facto* rights to fisheries were in some cases held by local lords, who controlled the waters adjacent to their manors. Nevertheless, most fishermen could make unrestricted use of the underwater grounds, either with or without a lord's consent. A contemporary chronicler reports that during the early 1600s oyster gathering and fishing was practised on a wide scale in the Oosterschelde near Zierikzee, 20 km northwest of Yerseke. Although the proprietors had prohibited exploitation of the banks, poaching was very common. Soon afterwards, according to the chronicler at least, the natural oyster beds there were depleted as a consequence of the reckless assault on this marine resource by human predators. Some enterprising Zierikzee merchants started to import the bivalves from England and Scotland and stored them in pits for a short time until they could be marketed (cf. Boxhorn 1644). Apparently, however, the prodigious reproductive potential of the species caused a remarkable recovery of the stocks soon afterwards.

In 1658, the provincial government of Zeeland granted

permission to a Zierikzee inhabitant to plant oysters on a plot in the Oosterschelde river. Several other entrepreneurs shared this privilege in subsequent decades. Although they held exclusive access rights to the plots where they had planted oysters, other fishermen were quick to steal the costly commodity at unseasonable hours.[1] McCay (1984) points out that this response to the enclosure of the piscatorial commons is cultural: the fishermen faced being forced out of waters to which they held customary rights and the only viable strategy to hold on to them was to continue fishing, albeit illegally. Because the streams in this area were not policed, their tactics proved to be successful and soon the zest to plant oysters ceased.

During the 18th century, the government of Zeeland switched several times between permitting free fisheries to all fishermen in the province and restricting entry through the issue of special permits. Without such a permit it was forbidden to exploit natural oyster beds or to plant spat or yearling oysters on new plots. The latter situation was often protested by the oystermen, who sent a flood of letters and requests to the governing body, yielding no results, however. Their initially futile attempts to restore open access furthered the piracy culture and by the end of the century free entry was re-established, although oystering was only allowed during a limited season (from October until March).

Fishermen vigorously vindicated their rights to the watery commons until the late 19th century. But as a matter of fact unrestricted entry to the Zeeland estuaries was fictious. The ethos of local fisher folk provided them with a model for the distribution of access rights to marine resources and their usufruct. They regarded the fishing grounds in the vicinity of their residence as their exclusive domain and occasionally tried to keep other, extralocal, fishermen from exploiting such ecological niches. The established oystermen did not hesitate to use violence against outside intruders who cast their dredges on these beds. Yersekers, for instance, successfuly defended 'their' oyster plots when fishermen from the neighbouring town of Tholen, one of them armed with a gun, tried to catch oysters there in 1837 (cf. van Ysseldijk 1973, p. 495).

Several anthropologists have noticed that "commons" are not a truly free resource. Moerman, for example, writes that "many tribal and peasant societies have customs and traditions which, in effect, control the freedom of the marine commons, and which, thereby, protect marine resources against excessive exploitation" (1984, p. 52). This applies to inshore, lake and riverine fisheries in particular. Taylor (1987) contends that the Irish Teelin Bay was a communal property resource rather than a common one. Similar cultural orientations can be found elsewhere, too. Indigenous forms of resource management can be very effective. Yet, when outsiders do not respect the traditional rights and customs of established fishermen, it is likely that a "tragedy of the commons" will occur. These intruders will usually try to monopolize access to fishing grounds to which they themselves hold customary rights, while they also seek to gain entry to other ones elsewhere, especially so in times of scarcity (see, e.g., Acheson 1972, 1975, 1979; Levine 1984). This ambivalent attitude towards territoriality is little understood so far and has yet to be scrutinized. There exists, however, no innate behaviour of fishermen which ultimately leads to over-exploitation of common marine resources.

This does not mean, however, that problems of over-exploitation were (and are) non-existent, on the contrary (see, e.g., the example mentioned above). Fishermen have often increased pressure on marine resources when their income dropped or when their number rose. Developments in the wider society also contributed to resource deterioration. In Europe, for example, many natural oyster beds were depleted by the latter part of the 1900s as a result of the boost to consumption provided by the steadily improving standard of living and the opening up of new markets, linked to the fishing villages by railway networks. Soon the demand for oysters rose, as did the prices paid. This dramatically increased the number and efforts of oystermen who fished or gathered what remained of the once rich resource.

The Zeeland estuaries were appropriated by the state in the early 1800s. The management of fisheries was assigned to the Board of Fisheries for the Zeeland Streams in 1825, which introduced some regulations pertaining to fishing gear and methods, closed seasons, and the size of marketable oysters, and demanded a small licensing fee of boat-owners and shellfish gatherers. Although the waters have been patrolled ever since, poaching was still quite widespread. Those without a boat were often fined by policemen, because they could not afford to pay the three guilders for the required license, but needed the additional income from oyster sales for their subsistence. Due to the potato famine of the mid-1840s, many poor families headed for dire straits and had to be supported by public assistance committees. The skipper-owners, often working with a family crew, were just slightly better off. Many Zeelanders emigrated to America during these years, several of them ending up in West Sayville (cf. Taylor 1983). Fortunately, the ecological conditions in the Oosterschelde were very favourable for the reproduction of oysters, so that the remaining fishermen were able to continue their maritime pursuit.[2] Elsewhere in Dutch waters, the natural oyster beds disappeared by the 1860s, but in the Zeeland streams this was not the case, although the yields declined. By the

[1] In 1661, the Federal Government issued a publication announcing measures against oyster poachers, but these did not yield the intended result.

[2] These favourable ecological conditions include high water temperatures (spawning requires temperatures of over 16°C), high and constant salinity, stable bottom conditions, and sufficient food (phyto-plankton).

end of this decade, the island of Zuid-Beveland was connected to the mainland by a railway-dam, which facilitated communications and linked Yerseke to inland urban markets abroad and at home.

Due to the depletion of natural stocks, the government encouraged experimentation with oyster farming. A small group of urban capitalists, anxious to invest their savings, tried to lease parts of the underwater grounds in the Oosterschelde near Yerseke. Some of them had studied oyster cultivation methods in the French Bay of Arcachon. After several attempts to acquire exclusive rights to certain plots, they were finally successful in 1870, when the Minister of Finance decided that the Yerseke Bank, an extensive natural oyster bed, would be leased at a public auction. This decision was vehemently contested by the oystermen, since they felt that they would not be able to obtain the best and consequently most expensive plots.[3] Their protests were in vain, however, and the Yerseke Bank was divided into parcels, five to ten hectares in extent, which were leased for ten year periods with the possibility of renewal for another five years (see Figure 2).

OYSTERMEN AND LIMITED ENTRY

The first public auction was held in Tholen, on May 6, 1870. Many entrepreneurs, the majority having an urban background,[4] attended the meeting and bid with alacrity. Most oystermen tried to secure the right to one or more parcels as well, sometimes forming partnerships so as to be able to pay the lease fees. Nevertheless, a large number of them could not afford to do so. They had to find a job with one of the newly established oyster companies or, if they cherished their independence, exploit the still free grounds or turn to musseling.

Yerseke, in former days a small agricultural village with just a score of fishermen, soon became the centre of oystering. Most of the entrepreneurs and companies operated from this village, because it was nearest to the underwater parcels and linked to an international railway network. The latter condition was vital, since the Dutch shellfish market was of little importance. The new method of oyster cultivation, using limed roofing tiles as collectors for oyster spat, required many hands. Within a decade the village population doubled to 2000, and by the 1890s had doubled again. Most migrants were impoverished tenants and landless labourers, who had worked on farms in the neighbourhood but lost their jobs during the agricultural crisis of the last two decades of the 19th century. Thus, both push and pull factors contributed to the rise of Yerseke as a shellfish centre.

Within an extremely short span of time the social relations of production in the industry were transformed completely. From a relatively egalitarian business—all oystermen being independent, having equal access rights and possessing similar means of production—oystering turned into a strongly stratified one. Among the first to be victimized by the new system were the oyster gatherers, who could no longer exploit the tidal flats. Neither could poor oystermen remain independent. Even if they were able to lease a cheap parcel it was usually only suitable to 'catch' oyster spat, which had to be sold, often at low prices, to those who had access to better plots, where it would grow up to a marketable commodity in four to six years. Locally, these men were known as 'tile farmers' (*pannenboeren*). Those who profited most belonged to the wealthy outsiders, who invested in the lease of the best parcels, boats, oyster sheds and storage basins. They were also in a position to develop a network of customers in England, Belgium, France, Germany and even Russia. A handful of these entrepreneurs, among whom the founding fathers of the industry, Pompe van Meerdervoort and Groeninx van Zoelen, combined oyster farming and shipping and often engaged over a hundred seasonal labourers during the campaigns. They were the undisputed 'oyster barons.' The social consequence of the state-supported lease system was an extremely unequal distribtution of access rights, means of production and income and the creation of social cleavages. The outcome was an odd amalgam of urban financiers, absentee oyster barons, companies, planter-shippers, independent planters and dredgers, tile farmers, foremen, labourers (both male and female, with many children lending

[3]In a Royal Decree of February 25, 1870 it was stipulated that the lease by public auction should not be to the detriment of existing oystermen. Once the new system was introduced, however, this condition was neglected.

[4]At least five of these wealthy urban entrepreneurs, several belonging to the aristocracy, resided in the country's capital, The Hague. Others lived in Ridderkerk, Bergen op Zoom, and Goes. The majority were members of the Dutch Society for the Promotion of Industry (*Maatschappij ter Bevordering van Nijverheid*). Since the early 1860s, this institution had shown an active interest in the introduction of oyster culture in The Netherlands. It initiated a lobby for the privatization of parts of the Zeeland Streams. In its journal and during meetings the Society depicted oyster culture as a lucrative branch of trade. This explains why so many outsiders leased underwater plots in the Oosterschelde and invested large sums of money in the oyster industry.

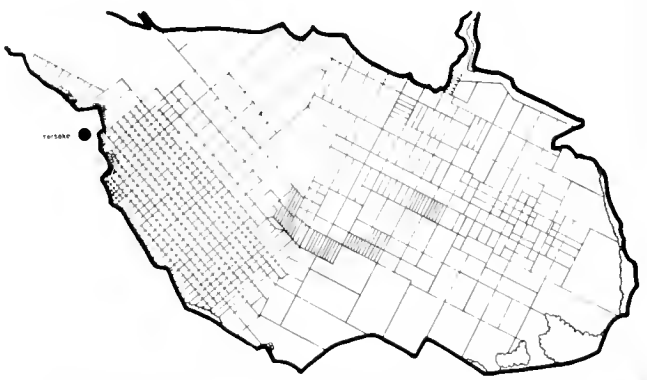

Figure 2. Shellfish plots in the basin of the Oosterschelde, circa 1874.

a hand) and artisans, like coopers and shipwrights. They were all in one way or another dependent upon each other. Nevertheless, the power balance was clearly to the advantage of shippers and planters, who could wield their influence over tile farmers and labourers, whose leverage was minimal.[5] In the preceding years, the oystermen had defended their customary rights by means of poaching. But after the introduction of the lease system, the state tightened up its supervision.

Initially, oyster farming proved to be rather successful. Formerly, the larvae of the bivalve had but little chance to survive. The roofing tiles were particularly suited for the spat to affix to and grow. Millions of tiles found their way into the estuary and when the seed oysters had the proper size the tiles were collected during low tide and brought ashore where the young bivalves were detached with a knife and relaid on certain plots until they had reached a marketable size. This semi-culture yielded far better results than the exploitation of natural beds. In the years prior to 1870, the number of marketed oysters hardly ever exceeded one million, while by 1875 it was 35 million (see Figure 3). During these first few years, conditions were extremely favourable, with several warm summers producing an enormous spatfall and foreign competitors lagging behind because of the depletion of natural oyster stocks.

Investors in the industry made good profits, since supply did not keep up with demand and prices were high. The independent oystermen and labourers benefitted as well. Many people were attracted by the success of those who had joined the mariculturists from the beginning and decided to make their fortune in Yerseke. At the ensuing public auctions the lease fees offered sky-rocketed. In 1882, for example, the sums paid for an acre of underwater grounds averaged Dfl. 27.50, roughly the price of the best agricultural soils, and a 1600% increase relative to the 1870 average lease fees. The highest sum paid amounted to Dfl. 9150 for a park of ten hectares. It was absolutely vital that one could lease a fine plot so as to be able to plant oysters and make money on investments. That is why people started outbidding each other at the auctions.[6] The high profit margins of the first decade of oyster culture created an image of Cockaigne, to be found on the shores of the Oosterschelde. By 1886 nothing remained of the free fishery there. The state, as owner of the Zeeland streams, collected the fees and lined its coffers. It also collected taxes and benefitted from the export trade with other European countries. The introduction of limited entry legislation

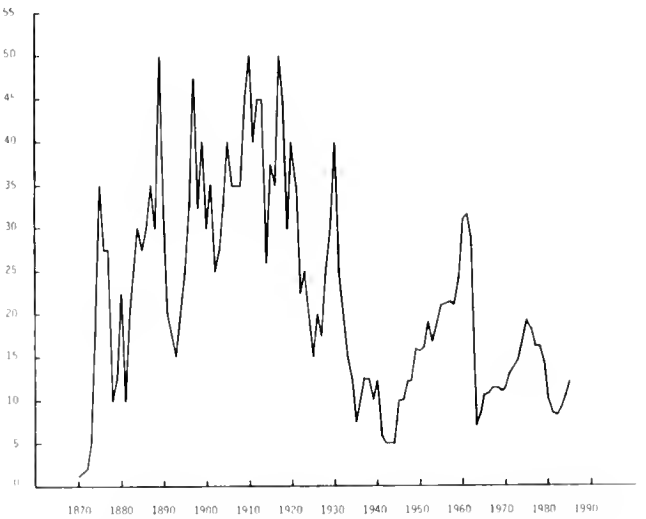

Figure 3. Production of marketable oysters (in millions).

contributed tremendously to the capitalization and industrialization of the oyster industry and to the boom in production.

Yet it was, paradoxically enough, this transformation in the mode of production which would cause problems. The established planters and shippers, as well as the newcomers, had expectations beyond what was reasonable. In their competitive struggle to gain access rights to the parcels, they lost sight of the potential risks involved in the enterprise. They restricted their view to earlier experiences and were too optimistic about the future. Hence, many of them over-invested, especially those companies which were financed by shareholders who hoped to make quick money. Some entrepreneurs sold their businesses at record prices to newcomers. Although access rights to the plots were exclusive, the government did *not* impose restrictions on the number of oystermen. In that respect it maintained a *laissez-faire* policy. Everybody who had been able to lease a parcel could set up his own business. By the mid-1880s, hundreds of oystermen and companies exploited the Zeeland waterscape. Due to the heavy lease burdens, the diffusion of knowledge and experience and, consequently, increased bivalve production, the high profit margins soon shrank to minimal ones or even turned into losses. The participants in the game were caught in a downward spiral. Because the returns on their venture dropped, they tried everything to increase oyster yields. Supply rose and oyster stocks boomed, but with a saturated market demand lagged behind, so prices were low. This dealt a death blow to many oyster companies, which went bankrupt because they had high overhead costs and the shareholders did not want to await possible profits in the long run. The large-scale capitalist oyster barons tried to increase production and reduce their costs by turning to other methods, for example by scattering cockle shells as collectors. This was less labour-intensive, and many labourers were sacked. It had

[5]McCay (1984) and Taylor (1983) describe similar processes pertaining to Shoal Harbor (pseudonym) and West Sayville, respectively.

[6]The public auctions were held in taverns, which stimulated excessive drinking and, consequently, reckless bidding. Jealously, distrust and sometimes even open hostility also encouraged oystermen to outbid each other.

consequences for tile farmers as well, since the demand for their spat dwindled. This caused a second exodus to the United States of America (and to Argentina as well) during the late 1880s. The small-scale planters, often leading family-businesses, proved to be very flexible. In bad times they had two options: either they could increase production, or they could curtail consumption to hold out for a while until better times. These two strategies were not mutually exclusive.[7]

To make things worse, the quality and growth of the bivalve deteriorated and mortality rates increased. The oystermen requested a scientific investigation to establish the causes. The state's fishery biologist, Dr. Hoek, concluded that, due to the overproduction, the stocks were greater than could be sustained, given the amount of phytoplankton in the estuary. They had to be reduced drastically to escape further deterioration (cf. Hoek 1902). As a matter of fact, this was accomplished in the early 1890s, not by human intervention, but because severe winters diminished the oyster population.[8] The elimination process in the bivalve industry, therefore, gained new impetus. At the same time the lease fees dropped so that the family-firms could gain access to better plots and play a more prominent role in the industry. Henceforth, the remaining entrepreneurs were slightly better off, but problems kept pursuing them. In 1905, for example, in England several people died after eating oysters contaminated with typhoid and consumers refused to buy the bivalves. As a result of this 'oyster scare', British oystermen dumped their yields on the European market at very low prices. The Zeeland oyster dealers temporarily lost many of their customers. The state merely collected the lease fees and, apart from demanding a certificate of purity for every marketed barrel of oysters, did nothing to help the ailing industry.

FURTHER DECLINE OF THE OYSTER INDUSTRY

Shortly after the outbreak of the First World War the state changed the lease system. Although The Netherlands maintained a strict policy of neutrality, the planter-shippers could not export their commerce to the traditional markets due to wartime hostilities and the imposition of trade barriers. As a result, fierce competition for a share of the shrunken market ensued. Prices dropped and exchange rates were low. The government recognized the problems and abandoned its *laissez faire* policy. The public auction was partly abolished and, instead, a new lease was introduced. The fees were now calculated as a percentage of the gross proceeds. This was done at the request of the newly established Co-operative Oyster Marketing Organization (*Cooperatieve Vereniging "Centraal Bureau voor den Verkoop van Zeeuwsche Oesters"*, abbreviated COCZO), which was supported by the government and joined by a fair number of planters and dealers.[9] This voluntary association sought to (a) restrict production, (b) coordinate oyster sales by allocating quotas to its members and (c) set minimum prices. The new leases applied only to its members in exchange for the self-imposed quota system. Initially, it was rather successful, but soon the planters and planter-shippers who had not joined sold their oysters at a lower price, thus undermining the aims of the COCZO. Several members of the co-operative started to sell their oysters clandestinely under the minimum prices as well, while they still enjoyed the advantages of the new lease. They did so because the independent oystermen sold all of their stocks, in contrast to the members of the COCZO who could only sell the permitted quantity and were consequently often left with vast amounts of unsalable oysters. More and more oystermen withdrew their membership and the co-operative had to be liquidated in the early 1930s. Thus, the COCZO was not able to solve the resource management problems in oystering.

During the 1930s, three factors determined the development of the industry. The first was an ecological calamity, viz. a serious outbreak of shell disease and the proliferation of the slipper limpet (*Crepidula fornicata*). This gastropod intruder competed for space and food with the oysters. Both plagues were facilitated by the presence of huge quantities of cockle-shells, by then the most important collectors for oyster spat (see Figure 4).[10] The second factor was the general economic crisis in the capitalist world during the period under consideration, exacerbated by the widespread proclamation of tariff-barriers. The third was the growing competition from English and French oystermen. England had always been an important market for the Zeeland oyster shippers, but British and French oystermen took over their share.

The government imposed a ban on the use of cockle shells and imported French yearling oysters to aid those planters who had lost a large percentage of their stocks. In order to secure a sufficient supply of oyster spat and year-

[7]Eric Wolf writes that peasants follow these strategies in order to balance "the demands of the external world against the peasants' need to provision their households" (1966, p. 15). This 'peasant dilemma' applies to small-scale fishermen as well.

[8]The species *Ostrea edulis* can endure water temperatures as low as minus 1.5°C for several weeks in succession, provided it is safely situated in deeper waters.

[9]In 1916, the year of establishment, 113 planters and planter-shippers joined the COCZO. Membership peaked in 1919 with a total of 128 members. In subsequent years, this number steadily decreased to 16 in 1934, the year of liquidation. During the period under consideration, approximately 180 oyster planters and planter-shippers exploited the Zeeland waterscape. Thus, in its heyday, 70% of the oystermen joined the co-operative.

[10]Cockle shells disintegrate quite slowly. When the underwater plots are not cleaned regularly, the debris can become a potential seat of diseases. This is exactly what happened in the 1930s, whereupon the state forced the planters to clean their plots.

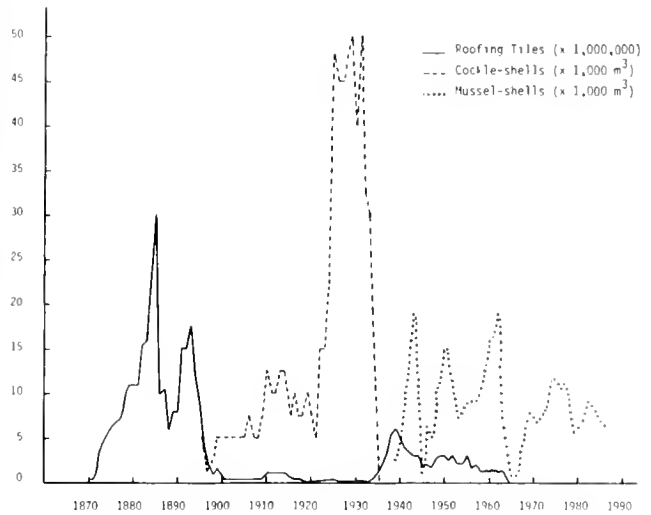

Figure 4. Use of different spat collectors.

ling oysters, the state provided financial support to unemployed labourers who wished to become tile farmers. The local authorities supplied these men with roofing tiles, while the state gave them access to parcels near the shore which had not been used since tile farming was abolished. Further, shippers had to join the Dutch Fishery Marketing Board (*Visscherijcentrale*) and were not allowed to sell under the minimum prices set by this body. This last regulation was, however, already repealed a year after its introduction in 1934.

The situation improved in the latter part of the decade, but the reintroduction of tile farming was not a success. The leading planters started to scatter mussel shells as colectors,[11] and also imported young oysters from Brittany. This considerably reduced the bargaining power of the tile farmers, because they were subject to the prices planters offered and these were usually very low. One of the tile farmers phrased it this way:

> "We could only lease those plots which were suitable for catching spat, not those fit for growing marketable oysters. So, eventually, you just had to sell. And there were many of us. So when supply was large, prices were low, you just had to accept that. If you did not want to sell for the money a planter offered, he would say: 'Well, you'll come back when you're hungry'. "

The tile farmers had sufficient foresight to realize that it would be economically safer to rear their oysters to a marketable size and export them themselves. It was, however, difficult to acquire good quality plots, for these were all in the hands of the established companies and planters.

During the Second World War, oystering came to a virtual standstill. Many boats were confiscated by the German occupiers and a large number of oystermen refused to sell oysters to them, so they had to stop farming the bivalves. The Germans replaced the lease system by a fixed yearly rent, calculated in terms of the estimated value of the plots. It was also regulated that the entry rights could not be transferred to other oystermen, as was the practice heretofore, other than by the agreement of the Secretary General of the Department of Agriculture and Fisheries. Lastly, the allotment of parcels became based on the need of individual oystermen and companies.

These regulations were adopted by the Dutch government after the war ended. Gradually the industry recovered from the disruption of these years. Nevertheless, the position of the tile farmers continued to be difficult, while the labourers benefitted from collective bargains. The associations of planters and shippers gained a foothold in state-level fishery organizations so that they were able to defend their interests. For the first time, too, potential newcomers had to wait for existing oyster farmers officially to relinquish their plots before getting a chance to rent a plot for themselves.

New problems soon assailed the Zeeland population. In February 1953, gales and exceptionally high tides in combination with a neglect of dike maintenance led to a tragedy. In many places dikes breached. Several polders were inundated, 1850 people drowned and material damages were enormous. Five years later, the government decided to dam off all Zeeland inlets, with the exception of the Westerschelde. Generally, the Zeelanders agreed to the plan, but the oystermen faced the death blow of oystering, since the Oosteschelde was the only body of water in The Netherlands where oyster cultivation was possible, apart from the marginal activities in the Grevelingen (see Figure 1). This government measure caused a lot of uncertainty, especially among the residents of Yerseke. The local authorities and those involved in the shellfish industry tried to draw attention to their problems. They approached representatives of political parties and the media. The only result was sympathy, without concrete promises that the matter would be reconsidered.

Then, in 1963, an extremely harsh winter decimated the oyster stocks; only 5% survived.[12] Most planters, and all tile farmers, decided to quit their business and accept state indemnifications, which would have to be paid anyway in the event of closure of the Zeeland streams. Some turned to musseling, while others set up new ventures, like chicken farms and mushroom nurseries. The labourers could easily find industrial employment, since it was a period of prosperity and many factories required workers. Ten Yerseke

[11]Mussel shells were purchased in vast quantities from the local canneries. Their advantage over cockle shells is that they disintegrate quite rapidly, forming no potential seat of diseases which can contaminate oysters.

[12]In the winter of 1962–63, the number of days with water temperatures below minus 1.5°C amounted to 71. Under these extreme conditions, 95% of the oyster stock died.

oyster planter-shippers, however, wanted to continue their operations as long as possible. In an attempt to keep the trade going, they imported large quantities of four-year-old oysters from France, Italy, Ireland, Norway, Portugal and other countries to relay them on their parcels and market them one year later. In addition, they scattered mussel shells to catch spat. Because supplies were scarce and competition was minimal, they could make more than a decent living and rented many parcels relinquished by those who had collected their indemnifications.

In 1974, the government altered its policy and decided that the Oosterschelde would not be shut off from the North Sea completely, so that oyster cultivation could continue. This change of state policy has to be understood against the background of democratization in the wider society since the mid-1960s. Environmentalists and fishermen ventilated their grievances over the proposed closure of a unique waterscape and gained the sympathy of a large proportion of the Dutch population. The question whether to dam the Oosterschelde was one of the issues in the general election of 1973. The coalition government which took office decided not to dam off the inlet completely. In 1976 Parliament approved the construction of a storm-surge barrier, which maintained the influx of fresh seawater.

This left the remaining oyster planter-shippers, all members of the Association of Oyster Exporters, in a very strong bargaining position. Firstly, they rented the lion's share of oyster plots. Only a few oyster planters had continued to rent some plots, without using them, however. Secondly, as the sole representatives of the oyster industry, they advised the civil servants of the Ministry of Agriculture and Fishery. Thus they were able to monopolize entry to the parcels and for several years in succession prevented other oystermen from regaining access to them. These former oystermen established an association to defend their interests. But soon yet another association was established, so that factional concerns prevented them from obtaining serious leverage. Since the Association of Oyster Exporters, initially at least, was the only body which advised the government in matters pertaining to the oyster industry, it was able to highlight its own interests.

In short, after 1963 the Zeeland oyster industry fell into the hands of a limited number of oystermen, who rented extensive areas of underwater grounds—a situation often portrayed by economists as being ideal to end resource management problems. But was this the case? The answer is negative. Against the advice of the State Institute of Fishery Investigation (RIVO) the shippers imported French oysters and planted these on plots in the Oosterschelde. In 1980, the RIVO established the fact that the oysters were affected by a parasitical disease, *Bonamia ostrea*. Consequently, the state banned oyster cultivation in the Oosterschelde. This was an unintended consequence of leaving the oyster industry in the hands of those who were, in the first place, merchants. Their opportunistic behaviour shows that transit trade was what they were after, and not the restoration of oyster populations in the Oosterschelde. Their limited mental horizon almost brought about the extinction of oyster cultivation in The Netherlands.

Accidentally, the Grevelingen, which was already dammed but later was provided with a sluice to let in fresh seawater, proved to be an ecological 'miracle' at the same time. The flat Zeeland oyster, thought to be exterminated in the 1963 disaster, proliferated in large numbers there. The Grevelingen is thus now the only body of water in The Netherlands where oyster cultivation is practiced. This is done by the ten planter-shippers of the Association of Oyster Exporters, in addition to another five who have gained access. The yearly yields of marketable oysters are approximately 10 to 12 million. Other former oystermen are trying to get permission to resume their activities as well and they have waged a war against the aforementioned association. All interested parties have connections at the highest political levels now and parliament has discussed the matter several times, without concrete results. The oysters in the Oosterschelde are still contaminated with *Bonamia ostrea* and many former oystermen are waiting to regain access to oyster plots, either in an Oosterschelde free of diseases, or in the Grevelingen. The situation is further complicated by the fact that the Grevelingen is also used by eel and sports fishermen, and they fiercely oppose the attempts of oystermen to get entry to plots in this saline lake.

CONCLUSIONS

The Zeeland estuaries have long been a common property resource, or rather a communal one, since local fishermen held customary rights to natural shellfish beds in the vicinity of their residence. In the latter part of the 19th century these banks were parcelled out and leased to the highest bidders at public auctions. This lead to a rapid industrialization and capitalization of the industry and a multiplication of oyster production. At the same time, however, the limited entry legislation had as its consequence that the social relations of production were transformed completely. From a relatively egalitarian occupational community of oystermen it turned into a strongly stratified industry. The allotment of exclusive access rights was certainly not a panacea for resource management problems, in spite of the initial boom in oyster yields. Since there was no restriction on the number of newcomers overcapitalization and overproduction ensued, leading to resource deterioration. But even with a small number of planters and shippers, as in the years after 1963, resource management problems continued. These problems are, however, not inevitable. Restoration of oyster populations in the Oosterschelde, once they are free of *Bonamia ostrea,* is possible. The future participants in the Zeeland oyster industry must co-operate with each other as well as with fishery biologists

and state institutions in order to ensure its successful expansion. Limited entry alone—in the sense of exclusive access rights and a restricted number of oystermen—is at best a palliative for resource management problems. This case-study should convince fisheries managers that privatization of fishing grounds is not, in itself, a sufficient management tactic.

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OYSTER AND SHRIMP PRODUCERS IN ESTUARINE AREAS OF THE GULF OF MEXICO ECOLOGICAL CONSTRAINTS, ECONOMIC INCENTIVES AND CONFLICTUAL MANAGEMENT[1]

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ABSTRACT Five major estuarine areas sustain the conduct of fishing activities in the Gulf of Mexico. In spite of strong similarities, mainly based on the exploitation of two major species, oyster and shrimp, each area is characterized by a differential social and economic basis in which the growth of capitalism generates conflicts of various intensity. The aim of this paper is to show how, in Alvarado and Ciudad del Carmen, opposite forms of resources management, partially rooted in some specific ecological features, arose from different forms of capital management and political power of groups of producers.

KEY WORDS: Oyster fishery, Shrimp fishery, management.

INTRODUCTION

Mexico occupies respectively the fifth and the sixth rank in oyster and shrimp fishing at the world level.[2] It therefore presents a significant case for the discussion of shellfishing management problems and of the ways social anthropologists could contribute to their solution. In this paper we would like to underline some of the present-day features of shellfishing and aquaculture industry in the Gulf of Mexico, focusing on two major fishing centers, Alvarado in the state of Veracruz and Ciudad Del Carmen in the state of Campeche.

We will begin with a brief historical outline of the human occupation of the area, emphasizing the local importance of economic competition even before the advent of industrial capitalism and then compare oyster and shrimp fishing in each community. In addition to pinpointing those contrasts due to their respective characteristics as forms of labor, we will show the degree to which, internally, and externally, their conduct is rendered conflictual by an increasing competition between producers whose political weight varies according to their level of capitalization. Our concluding remarks will underline the need for a better understanding of the links between shellfishing and related activities and of the larger social division of labor in the formulation of management policies. We will further suggest some ways in which maritime antropology might make a more effective contribution on the development scene.

I

Estuaries and Shellfishing in the Gulf of Mexico: History and Competition

Along the Gulf of Mexico are located five major estuarine areas of variable size.[3] Occupying an intermediary position between the coastal sea and the hydraulic basins of the hinterland, these areas are submitted to periodic overfloodings the bio-chemical effects of which are essential to the survival of both vegetal and animal life. Carrying a lot of nutrients, favoring changes in the water salinity, creating upwelling movements in zones of contact between fresh and salt water, these phenomena sustain the growth, especially in their earlier phase, of almost 90% of the marine species of commercial value in the area, namely the shrimp.[4]

The richness of these ecological zones, well proven by the fact they still are today among the major fish production

[1]The research was conducted in the Gulf of Mexico area between June 1983 and December 1985 and gave place to stays of various lengths in the field. Supported by a grant from the Social Sciences Research Council of Canada (no. 410-83-1124), the research team was composed of Eduardo Lopez Estrada and Gisèle-Eva Côté for the study of Ciudad Del Carmen and of Daniel Buckles and Yvan Breton in the case of Alvarado. A preliminary report was produced in 1985 and distributed to various universities, research centers and other public institutions in Mexico (Breton y. et allii, 1985).

[2]In 1985, oyster catches reached a total of 42,669 metric tons with a value of 945,733,100 pesos while shrimp catches represented 74,599 tons with a value of 909,301,000 pesos (N.B. 1200 pesos = 1 $U.S.).

[3]These lagunas and estuaries are: Laguna Madre, Tamiahua, Alvarado, Ostiones y Terminos. For more detailed information on the features of Mexican lagoons and estuaries, refer to Kutkuhn J. 1966, Ayala C. A. y F. B. Phelger 1969, 1971, Lankford R. R. 1976, Yanez-Arancibia A. 1976 and Edwards R. R. 1978.

[4]In this regard, several pilot studies have been conducted in the Tabasco area, located between the states of Veracruz and Campeche in the Gulf of Mexico. They discuss in greater details the fragility of the estuarine areas. Toledo A. 1982, Allub L. y Michel A. 1980, Ramirez O. B. 1984 and Pietri R. y Stern C. 1985. The latter also makes useful parallels between the economic development of Mexico and the problems related to polution of ecosystems. Also consult Clime R. *et al.* (1980), Sada J. (1984) and De La Cruz J. L. and Reyna R. (1986) for the social consequences of ecological deterioration for lagoon fishermen of Tamiahua and Ciudad Del Carmen (Laguna de Terminos) and Mc Goodwin J. R. (1980) for the Pacific region.

centers in the Gulf of Mexico, is of significance to the problem under discussion. It is first responsible for the early human occupation of the region. In a pre-colonial economy in which the labor force remained the main productive factor, a location nearby a readily available source of food represented a highly adaptive device, a situation confirmed by archeological findings and oral tradition.[5] It also suggests, given the annual variations in production, that competition for the resource started long before the arrival of the Spaniards, though on a different scale. When the latter came into the area, also attracted by the avantageous location and ecological potential, they interacted with native people and modified to some extent the existing relations of production in the exploitation of the natural resources. Competition thereby acquired a different form. Even though no major technological change took place, except for the introduction of larger nets, property relations and conditions of access to the resource, progressively moulded by asymetric class relations in which ethnicity was determinant, all changed in ways whose influence is still visible today. In other words, before the strengthening of industrial capitalism, the consolidation of a mercantile economy oriented towards the fulfillment of both internal and external needs created a new basis for competition. In a country like Mexico where, over a long period of time, a large concentration of population had been in the remote highlands, access to and control of the estuarine areas in which shellfishing was an important economic activity represented for the mercantile European entrepreneurs important strategies in order to progressively transform the economy and adapt it to their commercial objectives. Not only were these areas adequate natural harbours, but they also gave access, through their internal hydraulic system, to inland towns and markets. At the same time, given the lack of ground transportation facilities in the lowlands, the control of the water streams was essential for the dispatching of agricultural and other goods to the metropolis. Increases in fishing production and in processing and marketing activities required a larger labor force whose recruitment was compulsory (importation of slaves from the Caribbean) or embedded into patron-client relationships very similar to what prevailed in the agricultural sector with the encomienda and the hacienda[6] systems. Local history abounds in events linked to fights among the natives, pirates, and Spanish representatives over the control of these areas during the 16th, 17th and 18th century. Some of these conflicts gave rise with time to quasi-prebendal types of domain, the existence of which is still a point of reference in present-day discussion of management issues.[7]

It was not until the end of the last century, however, that additional demographic pressures and new economic incentives brought significant ecological deterioration to these estuarine areas. The expansion of the sugar-cane industry, for which streams played a key-role in the waste disposal of the "ingenios", and the progressive discovery of petroleum wells along the Gulf endangered the reproduction of marine species to a level never reached before, confering to management issues an acuity which is an integral part of the producers' dilemma and of their claims and demands.[8]

What preceeds seeks to underline the fact that present-day competitive processes in the estuarine areas of the Gulf of Mexico have deep historical roots. The advent of industrial capitalism, leading to increased and more diversified production, undoubtedly stressed competition between producers exploiting natural resources and affected the conduct of fishing activities by endangering the reproduction of marine species. It would be misleading, however, to minimize the importance of competition and management problems in a former context in which an incipient mercantile capitalism, first based on a lavish nature able to support additional exploitative efforts, rapidly gave rise to numerous conflicts between producers. It generated competition not only for the access to and control of the resources, but also for the labor force and the commercial roads. In other words, as soon as the reproduction of capital became the major economic incentive, competitive processes emerged which subsequently moulded the ways in which ecological deterioration and more acute management problems took place.

These introductory remarks seem to us important when discussing management issues in a "common property" context such as fishing.[9] They draw attention to the neces-

[5]Cf. Ramos Hernandez M. D. 1977, Leriche-Guzman L. F. 1982 and Baez Z. and Marchal J. Y. 1986 for more extended information.

[6]The encomienda consisted of a domain granted by the Crown to individuals for a certain period of time, going from one to five generations. This system tenure mostly prevailed during the 16th century; succeeded to it the hacienda, a privately owned domain the lands of which were directly bought from the Crown

[7]Further ethno-historical research is needed to clarify the situation. For instance, in Alvarado people often refer to the Laguna Camaronera as a type of prebendal domain rented by the Ayuntamiento (local town council) to particulars who had to pay regular dues according to their volume of catches. The authorities could also impose a tax on maritime transportation since the lagoon was a natural link with the main town of Veracruz. Cf. Ramos-Hernandez 1972. People now living in the small community of "Camaronera" have developed a strong sense of belonging to their lagoon and jealously watch any intrusion from outsiders into their area.

[8]The petroleum industry, first located in Northern Veracruz, has significantly expanded into marine zones during the last decades. 55% of the Mexican total production now stems from the Sonda de Campeche, in front of Ciudad Del Carmen.

[9]"The Tragedy of the Commons" has been at the center of many debates between fishing experts areas the last decade. Rooted in the biological concept of "maximum sustainable yield", the common property theory in fishing rapidly acquired are an economic dimension which inevitably included social and political consequences. For more information on these debates, refer to Gordon H. 1954, Hardin G. 1968, Kearney J. 1984, and Guppy H. 1986.

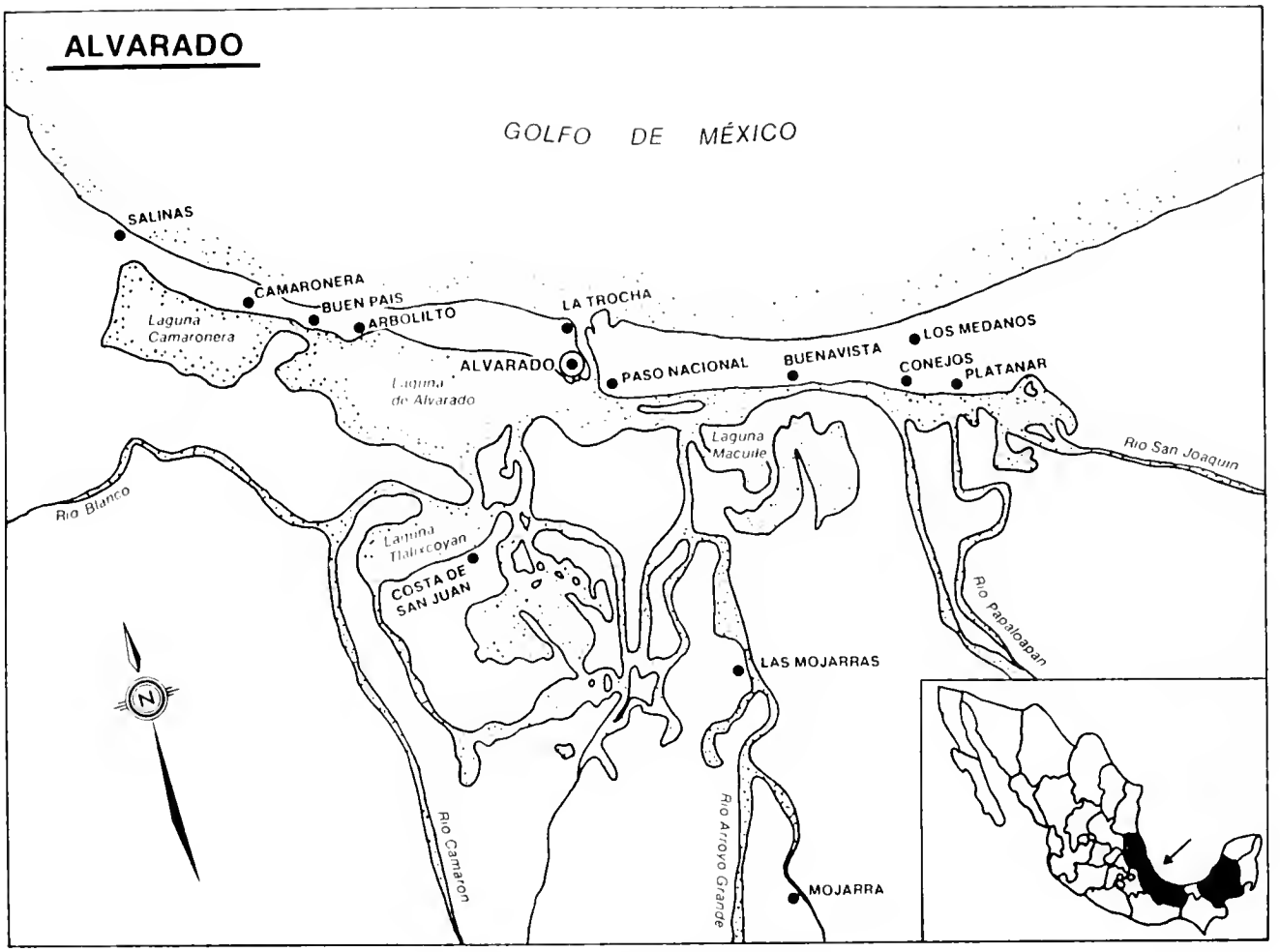

Figure 1. Alvarado and its estuarine region.

sity to conceive management issues not only by focusing on the natural resources but also by considering the human producers whose labor force remained, for a long while, the main source of energy for production. On the other hand, they stress the importance of reducing the illusion of the novelty of management problems in activities linked to the exploitation of marine resources. Too often, the bureaucratic and formalist devices employed in the formulation of a problem lead to solutions that make the problem appear to be a relatively new phenomenon and an inevitable if slightly negative, consequence of a largely and socially desirable progress. Such a procedure denies the long term cultural context in which the problem took form and further increases the dependance of producers upon external specialists who can therefore more easily impose regulations contrary to customary practices. Present-day issues in shellfishing in the Gulf of Mexico, though apparently related to and excerbated by recent economic and political changes in the conduct of fisheries, must, nevertheless, be grasped within a framework that takes into account their social and historical setting. This is the essence of the demonstration that follows.

II

Alvarado and Ciudad Del Carmen: Ecosystem and General Features of Fishing

The two estuarine areas directly concerned in this paper are those of Alvarado in the state of Veracruz and of Ciudad Del Carmen, in the State of Campeche. The region of Alvarado is characterized by a complex hydraulic system in which numerous rivers (Rio Papaloapan, Blanco, San Joaquin, Arroyo Grande), fall into various lagoons of irregular size, the largest being that of the Laguna de Alvarado with an approximate extension of 120 km^2. On the contrary, in the Ciudad Del Carmen region, rivers and streams (Rio Palizada, Chumpan, Candelaria, Mamantel), flow into a fewer number of lagoons among which that of the "Laguna de Terminos" is predominant, covering an area of 1400 kms^2. Presenting strong similarities at a general level as transitional zones between mainland and coastal sea, including numerous valuable species, these estuaries are, nevertheless, characterized by important geographical and topographic differences which generate a great variety of fishing techniques and of production units (cf. maps).

Differences also exist at the socio-economic level. The municipio of Alvarado comprises some 35,000 people, scattered in a dozen small communities throughout the delta,[10] the major concentration being found in the town of Alvarado itself, with 15,000 inhabitants. Except for small agricultural and cattle raising production-units in zones not too affected by the seasonal floodings, the majority of the population makes a living from activities related to fishing. About 3,000 producers, among whom 1,300 are members of fishing cooperatives,[11] work in the area, their production consisting, in addition to shrimp and oyster, in the capture of diversified species (chucumite, robalo, jaiba, lisa, lebranche) a good part of which is sold in the Mexico City markets, a situation well illustrate of the maintainance of the commercial relation that have existed since pre-colonial times.

About 200,000 people live in the Ciudad Del Carmen area, among whom 150,000 in the city itself. With a fishing population of 4,000 whose cooperatives' membership reaches 1,700 producers, the fishing activities, conducted with larger capital assets and better equipped boats, are concentrated mainly on the capture of shrimp on the open sea and oriented toward external markets, especially that of the USA. Low-capital fisheries concern only a reduced number of local fishermen and of fishermen of small neighboring communities (Atasta, Isla Aguada, Sabancuy) who periodically visit the area for the capture of oysters or of migratory species such as the jurel or the lebranche. In addition to this greater degree of specialization in fishing, Ciudad Del Carmen is now the major petroleum production center in Mexico, the extractive activities being concentrated on the Sonda de Campeche, on the continental platform just in front of the city. This brief presentation of the ecosystems and organizational features of fishing shows that parameters for competitive actions are somewhat different in each area. Though facing identical environmental problems, mainly pollution and depletion of fish stocks, producers are embedded in socio-economic organizations in which capitalism did not develop with a similar rhythm and intensity. Let us look more closely at the discrepancies generated by this situation and at its consequences in terms of management policies.

III

Oyster and Shrimp Fishing: the Cultural Dynamics

We have already mentioned that oyster and shrimp fishing are potential alternatives for many Alvaradeños or Carmelitas producers. Mexico being a country in which coastal aquaculture is not highly developed, most of the oyster catches are limited to the internal zones of the estuaries while in the case of shrimp, a migratory species, the catches are made in both the internal and coastal zones, and, at this level, there do not exist significant differences between Alvarado and Ciudad Del Carmen. However, the presence of estuaries characterized by generally similar features does not necessarily imply a uniform exploitative potential. For instance, the highly parcelled nature of the delta of the Papaloapan River in Alvarado, compared with the presence of a large lagoon (Laguna de Terminos) in Ciudad Del Carmen, allowed for an extended litoral which offers greater possibilities for oyster catches. On the other hand, the more numerous and larger connections between the Laguna de Terminos and the open sea explain why the shrimp industry has reached a greater level of consolidation in that area. Similar remarks could be made at the strictly economic level, taking into account the capital needed to obtain reasonable yields. Oyster fishing is conducted by small producers with a low level of capitalization and technology, while in the shrimp industry capital assets are already higher than the oystering in the interior zone, and reach a much higher level of investment in the open sea fishery.

Without denying the importance of these elements in explaining the difference in management issues in these fishing centers, they are not sufficient, however, to explain differences in intensity, direction and peoples' visualization of and feelings about them.

Alvarado has been a major fishing center since precolonial times. Its direct links with and closeness to Mexico City have provided it, at an early stage of its development, with good commercial opportunities. Forty-five per cent of its production is still being sold in the internal, national market. The richness of its estuary has for a long time attracted entrepreneurs who, during the colonial period, set up prebendal forms of domain similar to those prevailing

[10]These communities include between 130 and 1,700 people, with an average population size of 450. The most populated are located close to the national road leading to Veracruz or Tampico, the rest being scattered through the estuary, some of them described as "rancherias" (fishing stations).

[11]In Mexico, fishermen are grouped into three sectors: private, state and a cooperative sector. The cooperative (also called "social" sector) first emerged in the 20s. Under the regime of Lazaro Cardenas, at the same time that took place the nationalization of the petroleum industry and the extension of land distribution in the agricultural sector, the fishing cooperatives were progressively granted exclusive rights of capture for certain species. Starting with the spiny lobster in 1936, these rights were extended to the capture of oyster, abulon, octopus, squid, in 1937, and of shrimp in 1940. In 1941, was created the Bank of Cooperative Development. All these measures, however, were not accompanied by sufficient financial support with the result that most of the cooperatives had to rely on private capital in order to engage in production. In several cases, cooperatives members became proletarianized workers for private entrepreneurs who, otherwise, were not able to engage in the fishing of these species of high commercial value. It was not before 1970 that, with a greater and restructured state intervention following the nationalization of the 200 miles marine zone, that some cooperatives succeeded as economic actors. In 1985, there existed 1,200 fishing cooperatives in Mexico regrouping more than 50,000 producers. They form a wide range of production units going from groupings of a small number of artisanal fishermen, to ones which include a few hundred fishermen with sophisticated technology and large capital assets.

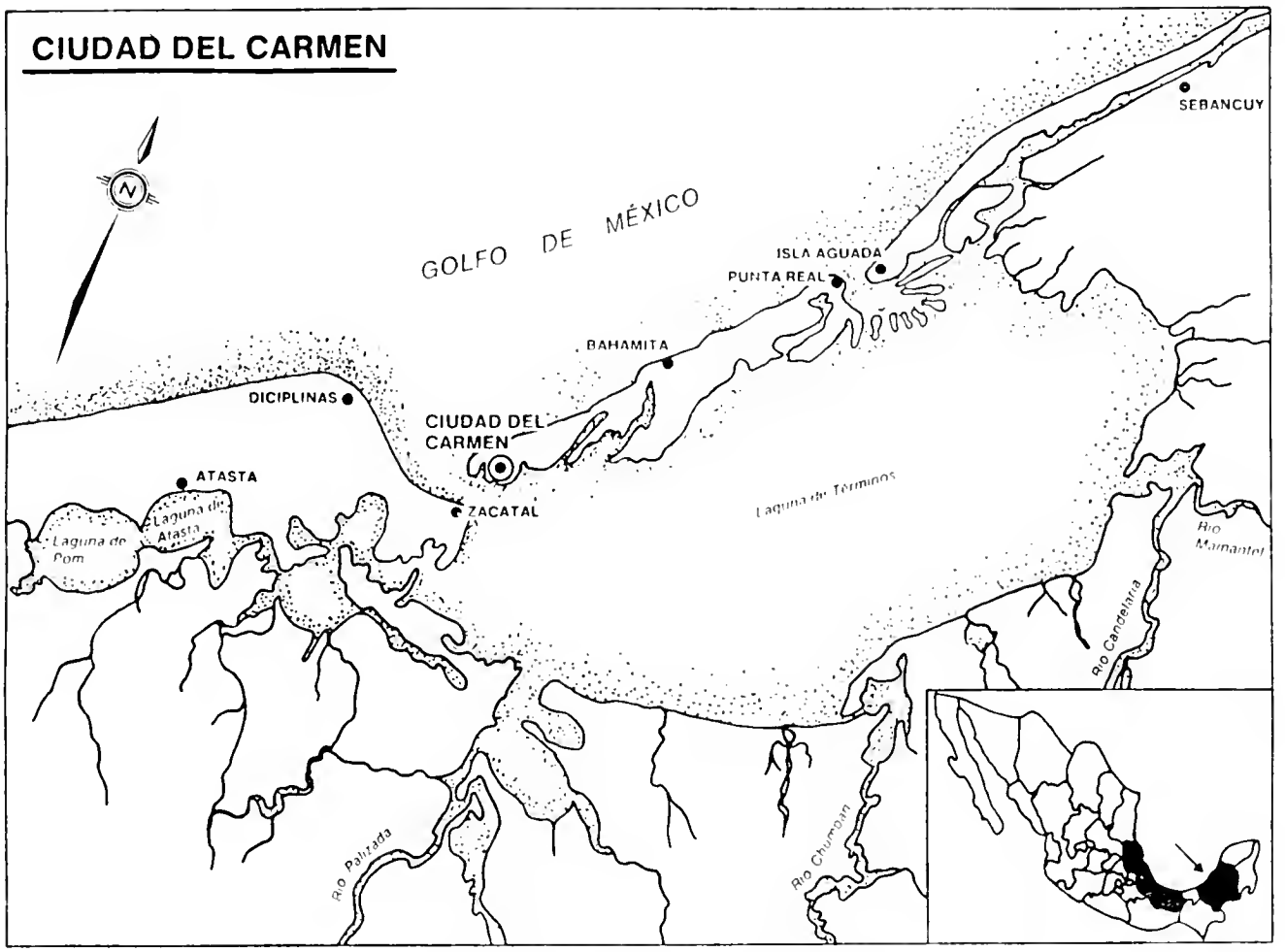

Figure 2. Ciudad del Carmen and its estuarine region.

during the "encomienda" period in the agricultural sector. When industrial capitalism in fishing, already present on the Pacific Coast at the end of the last century, reached the Gulf of Mexico in the 30s, it was faced with a social system in which pre-capitalist relations of production could not be easily destroyed. Shrimp fishing activities in the open sea, the branch of production that supported the growth of Mexican fishing capitalism, took place on a reduced scale in the area, the producers preferring to maintain a diversified production in which oysters and shrimp caught in the estuary kept their significance.

On the contrary, even with a significant historical basis of fishing in Ciudad Del Carmen, its levels of production remained low until the last decades. This situation was mainly due to the reduced population density of the area and to its remoteness from the major urban centers. However, when capitalist entrepreneurs, already engaged in the shrimp fishing on the Pacific coast, discovered new schools in the Gulf of Mexico, and namely in the Sonda de Campeche, Ciudad Del Carmen rapidly became a major production center with capital intensive production units, mostly controlled by outsiders and oriented toward a lucrative external market.

Even though in each community almost fifty per cent of the producers are cooperative members, the number of cooperatives as well as their internal features vary greatly. In 1984, Alvarado included 17 cooperatives, only four of which were fully engaged in deep sea shrimp fishing, the rest restricting their activities to the estuary and coastal areas. Among them, five were specialized in oyster fishing. In Ciudad Del Carmen, there existed at the same period 36 cooperatives, 17 of which were engaged in deep-sea shrimp fishing and only one of which clearly confined itself to estuary oyster fishing.[12] Since shrimp fishing in the open sea represented a highly intensive capital labor process, often totaling a few hundred thousand dollars, there is no need to insist upon the greater economic and political importance of its adepts compared to those engaged in oyster and

[12]Since 1982, the fishing cooperatives in Carmen became afiliated to two district federations, this situation illustrating the increasing conflicts between deep-sea and estuary fishermen.

shrimp fishing in the estuary. When both the historical and present-day features of capital are taken into account, there exist strong differences between the producers of the two communities. The nature of the labor process also entails management issues the intensity and the political implications of which vary greatly.

Oyster fishermen have to resolve problems related to the management of their lagoon (quality of seed-shells, levels of capture according to the market situation) and, overall, the issues are dealt with on an internal basis, among the members of the cooperative or among the cooperatives themselves. Management concerns and modalities are, however, different with the shrimp fishermen since that fishery is characterized by a marked opposition between the estuary and deep-sea producers. Since shrimp spend a good part of their juvenile phase in the estuary, catches in this area necessarily affect the level of production in the open sea. Therefore, management issues in this case are affected not only by concerns for the biological reproduction of the species, but also by the competing interests and political displays of two groups of fishermen characterized by different ways of fishery and levels of capitalization.

In Alvarado, the parcelled nature of the estuary, including numerous sectorial lagoons, has allowed the establishment of several independent communities which strongly identify themselves with the exploitation and the management of "their lagoon". In the most remote communities, people do not hesitate to drive out, "*manu militari*", new-comers who venture to exploit territories that they defined as local "common property". In the lagoons closer to the town of Alvarado, competition for access to the resource is entangled with more "official" juridical procedures, these areas being subjected to a more regular control by the fisheries officers.

With the progressive setting up of the deep-sea fishing cooperatives since the end of 1970, their representatives have made repeated requests to the authorities for the establishment of a permanent prohibition on shrimp fishing in the estuary. So far, they have not succeeded, and they must content themselves with the temporary "prohibitions" applied at different times of the year of different locations according to species of shrimp. The system is, therefore, highly flexible, opening the doors to frequent poaching. In spite of the efforts of the bigger cooperatives (supported by private entrepreneurs) to make of the estuary a sort of protected area for shrimp, the producers who exploit it, still representing a good part of the labor force in fishing, have succeeded in maintaining the pursuit of their traditional activities by combining informal and formal management devices. In addition to resorting to their "customary" rights, they argue that before the coming of "outsiders" in the days of the less intensive shrimp fishing in the continental zone, they were able to manage their resources and protect their main source of living.

These issues take on a far more drastic aspect in the Ciudad Del Carmen area. Given the size of the Laguna de Terminos, it was a lot easier for the "Carmelitas" entrepreneurs to convince the official authorities to establish, in 1974, a permanent prohibition on a shrimp fishing in the lagoon, thus favoring the possibility of higher catches in the open sea area. This action, which was rendered feasible by the fact that the main lagoon was not appropriated by "localities" or by "familiies" as in the case in Alvarado for the smaller lagoons, can be seen as a protective measure oriented toward the conservation of the shrimp species. However, since the action did not prevent larger fishing efforts in the open sea area, a situation encouraged by the high profits derived from the activity, it served to promote illegal fishing in the mainland area ("guateo" in Mexican terms). Excluded from a traditional source of income at the same time that potential revenues derived from it were increasing, and feeling that their political weight could not be of much help in dealing with the authorities, coastal and inland fishermen had to exploit an environment upon which externally imposed restrictive devices limited their efforts.

Some of these fishermen try to diversify their production according to legal avenues, but the whole area, even though it can be described as a protected area, is subject to increasing illegal practices detrimental to good management. It is therefore the radical elimination of previous customary rights of the inland fishermen, enhancing their economic precariousness, rather than their lack of environmental conciousness that explains the deterioration of the situation.

These cases show that the differences between the oyster and shrimp fisheries in the Gulf of Mexico cannot be grasped only with reference to the physical characteristics of the species. In addition to considerations of the larger ecological setting in which their conduct takes place, it is highly important to analyse these differences, and the management practices that accompany them, within a framework that gives proper place to the social features of capital. In the above cases, even though management practices and results present some striking similarities, they are molded in particular human contexts the components of which remain the major explanatory factors for the existence of a variable intensity and direction in management issues.

CONCLUSION

Shellfishing, Reproduction of Capital and the Social Division of Labor

We have so far examined the conduct of oyster and shrimp fishing in Mexico basing our assumptions upon the analysis of the situation that prevails in two fishing centers of the Gulf of Mexico. Although limited in space, these ethnographic examples illustrate the highly flexible nature of management problems in fishing and show that in the establishment of policies, a middle range controlled comparison in which socio-cultural factors are considered an integral part of the variables at work can be illuminating. Obviously, if transposed to the national level, our demonstration could be greatly enriched, given the features of the

regional division of labor in Mexican fishing.[13] But rather than entering into the examination of these regional variations, we would like, in conclusion, to draw attention to additional parameters that increasingly condition these fishing activities in Mexico, namely those related to State interventions and to the links between fishing and other branches of production.

As in several countries in which the nationalization of the 200 miles marine zones gave rise to a stronger State invervention in fisheries, Mexico is now characterized by a highly bureaucratic structure at all levels of the activity. In addition to creating State fish plants at the end of the sixties (Propemex), to setting up numerous credit agencies and to allowing an increased number of cooperatives in the seventies, the State even established a ministry specific to fishing at the beginning of the eighties. This does not mean, however, that all fisheries are given the same importance and interest. Since shrimp fishing has been at the core of the consolidation of fishing capitalism in Mexico, it represents the activity that received most attention from the State authorities. On the contrary, since oyster fishing always remained an inshore activity, concerning small producers and not representing an important element for the entry of foreign currencies, it has most of the time been considered as marginal even though in some areas it plays a non-negligable role in local and regional markets.[14] Amazingly enough, compared to shrimp fishing, there exists almost no credit program for oyster fishermen. Since both shrimp and oysters are to some extent exploited in the same areas (namely estuaries and lagoons), by neighboring producers, this situation creates a discrepancy that contributes to unbalance the success of management policies. In other words, both in Alvarado and Ciudad Del Carmen, the action of the State authorities concerning the management of oyster and shrimp fishing in the estuaries does not take sufficiently into account the social components of the communities. On one hand, as shown by the previous discussion, it gives little attention to the specific history of each locality, their management and control practices being molded within a common juridical framework supposedly applicable to any part of the country. We have seen, however, that due to their different social trajectories, producers in each community did not react in identical ways to State intervention. In one case, they have been able to partially maintain their customary rights; in the other, they were forced to accept fishing prohibitions but now frequently engage in poaching.

On the other hand, the fact that the State authorities think of management in terms of particular fishing activites rather than of specific fishing communities results in increased social cleavages and conflicts that destabilize their action. In the same community, producers who exploit oysters or shrimps in the estuary are subjected, in one case, to almost no regulation and, in the other, to increased pressures from the fisheries officers. In addition, compared to shrimp fishermen exploiting the estuaries, those involved in the open sea can benefit from a larger financial aid from the state given their stronger economic and political power.

What preceeds shows that by focusing their attention upon the human producers and their social circumstances, anthropologists could contribute more to the establishment of management devices. Without diminishing the importance of the natural resources or of the economic dimensions within fishing activities, our demonstration emphasizes the need for a better recognition of the weight of the producers themselves when management issues are involved. Their vision of fishing is not only oriented toward the future, it is also deeply rooted in history and very often, more than specialists, fishermen develop a relational approach in which the evolution of fishing is constantly paralelled with that of other activities affecting their ecosystems.

Many fishermen would not hesitate to assume that, even though the State has been seeking to promote the development of fishing, it has done little so far to prevent the growing presence of negative elements derived from other activities. For instance, given the extension of their hydraulic system, Alvaradeños fishermen are greatly affected by the pollution coming from the town of Orizaba and neighboring industrial centers. In addition to the presence of a papermill (Tres Valles) which regularly dumps caustic acid into the water streams, the major sources of pollution come from seven "ingenios" related to the sugar-cane industry. Since these plants generally operate between December and May, during the dry season, they accumulate large quantities of detritus that reach the productive zones in a concentrated way once the rains start again.

A similar and even more drastic situation prevails in the Ciudad Del Carmen area in which oyster and shrimp fishing management problems are more and more entangled in the conflicts generated by the expansion of the petroleum industry. Started in the year 1976, this industry has undergone accelerated development, more than 55% of the national petroleum production now coming from this area. In addition to causing significant changes in the community (the pop. went from 45,000 to 150,000 between 1970 and 1984) it directly affected fishing both in the deep sea and estuarine areas. In the latter case, the infrastructures linked to oil transportation are encountered in the vicinity of the most productive zone for oyster fishing, thus causing a noticeable decrease in catches in recent years.[15] Since the petroleum industry is Mexico's largest source of income, in a

[13]Cf. Breton Y. and Lopez-Estrada E. (1987) for a more detailed study of Mexican fisheries.

[14]One advantage in oyster fishing lies in the possibility of a planned production thus facilitating the good functioning of the cooperatives which are able to adjust to market variations.

[15]In 1984, PEMEX planned to establish 46 wells in the Punta de Atasta, close to the Eastern end of the Laguna de Terminos and the Laguna de Pom. The advent of the petroleum industry also caused a significant inflation in Ciudad Del Carmen. Cf. Uribe J. (1983) for more information on ecological deterioration caused by PEMEX.

country which now has one of the largest external debts in the world, it is doubtful that the negative effects of petroleum industry upon fishing will be reduced in the near future. Management policies in oyster and shrimp fishing are therefore highly conditioned and influenced by external elements which, in spite of their exogeneous status, cannot indefinitely be considered as independent variables. The Mexican case is highly convincing on this point.

Addressed to specialists of various disciplines interested in the development of fisheries, our paper did not seek to fully describe the ethnographic richness of oyster and shrimp activities in the Gulf of Mexico. Rather, we tried to pinpoint some analytical elements that from an anthropological perspective deserve attention. Hopefully we were also able to show that in the establishment of management policies, the social dimension of fishing, namely that related to the history of fishing capital in various communities, bears great significance for the understanding of the failure of some policies or of their rejection or partial acceptance by the producers.

Fisheries development programs are greatly influenced by the research conducted on fish populations dynamics, pinpointing their fragility and the constraints linked to their biological reproduction. This orientation lies at the core of the majority of actions undertaken by state agencies in fishing. Amazingly enough, however, even though fish and fishermen form part of the same ecosystem and management policies are supposedly aimed at bettering the economic situation of the producers, so far little attention has been paid to the social reproduction of fishermen.

The demonstration that preceeds seeked to illustrate how social anthropologists wishing to participate actively in the development of fisheries can potentially contribute to rectifying this situation.

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MUDDLING THROUGH THE CLAM BEDS: COOPERATIVE MANAGEMENT OF NEW JERSEY'S HARD CLAM SPAWNER SANCTUARIES[1]

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ABSTRACT This article describes the process whereby hard clam (*Mercenaria mercenaria*) spawner sanctuaries were created in estuarine environments along the New Jersey shore in an attempt to increase recruitment in the region. While the project was only a limited success in terms of this biological goal, this experiment in co-management involved complex and revealing socio-cultural interactions among a variety of constituencies and individuals who attempted to "muddle through" the problem solving process together. This article is principally concerned with analyzing and understanding what happened from an anthropological perspective. It thus hopes to contribute to our understanding of the reasons for the successes and failures of such cooperative efforts at fishery management problem solving.

KEY WORDS: *Mercenaria mercenaria*, spawner sanctuary, management

INTRODUCTION

This article is based on participation in an experiment in co-management that began in May 1985 with proposals to create hard clam spawner sanctuaries in the state of New Jersey. The argument behind co-management is that to achieve more effective and equitable systems of common-property resource[1] management, representatives of user groups, the scientific community, and government agencies should share knowledge, power, and responsibility (Pinkerton 1987, Kearney 1985, Jentoft 1988, McCay and Acheson 1987). It is very difficult to create a management program for a common-property resource that is: (a) equitable in its effects on different social groups and individuals; (b) based on knowledge and data that are adequate to the task of creating regulations that work; and (c) enforceable. Co-management should, in theory, reduce those problems by bringing the users directly into the management process rather than assigning them solely to the role of those being regulated. This assumes that users as well as scientists have knowledge and data that can help government officials better assess problems and devise solutions. It assumes that fuller involvement of users in the management process will reduce the political and equity problems that often arise from resource management efforts. Finally, it assumes that if users are more fully involved in management, they will be more likely to perceive the management system as legitimate and hence to comply with the rules and regulations developed (Jentoft 1988).

In the shellfish enhancement case to be described, co-management involved officials of the State of New Jersey's Department of Environmental Protection (DEP) in cooperation with clammers. It involved both in cooperation with scientists of different disciplines (biology, biochemistry, anthropology) and from both academic institutions (Rutgers University) and government agencies (several divisions within New Jersey DEP; the state Fisheries Development Commission; the federal National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory). Added participants were state and local politicians, county officials, and a marine extension agent.

I describe the inception and realization of New Jersey's hard clam spawner sanctuary project and discuss its problems and accomplishments. It will be seen that the hard clam spawner sanctuary was an imperfect instance of co-management. The involvement of clammers in the project was not enough, or not done well enough, to prevent or blunt conflicts among groups of clammers. It also did little to encourage adherence to the rules and regulations of the program. However, these and other failures and disappointments in co-management cannot be adequately explained by recourse to stereotypes of the inclinations of clammers, or state bureaucrats, or biologists, or even anthropologists. The structure of relationships among the people and groups involved and the way they viewed and interpreted each others' behavior were critical factors.

Finally, the knowledge and data provided by clammers and academic scientists were inadequate to the task of shellfish enhancement, at least in the short run. The scientists, clammers, anthropologists, and state officials involved in the project were confronted with the problem of decision-making in the context of scientific uncertainty and ignorance. For that and other reasons, the decision-making approach taken was that of incrementalism, or muddling

[1]By "common property resource" is meant a resource that has properties such that it is difficult for one user to exclude others from it, and the activities of one user can subtract from the benefits obtainable by another (Feeny *et al.* 1988; Ostrom 1986:604). It is important to distinguish such a resource from the cultural and legal regime that is also often called "common property." In fact, institutional regimes that concern such resources are comprised of variations ranging from totally open-access and unfettered use of a resource to various communal systems of controls over access and use to different levels and kinds of centralized government intervention (Ciriacy-Wantrup and Bishop 1975; Moloney and Pearse 1979; Bromley 1986). We have recently proposed the terms "open access," "communal property" and "state governance" for general types of regimes (Feeny *et al.* 1988).

through (Lindblom 1969, 1979). Probably more important than the clams transplanted and the spawn they emit into New Jersey's waters is the fact that this project resulted in the creation of a position in applied hard clam biology dedicated to reducing the uncertainty and ignorance that plagued the project. I suggest, however, that the real challenge is to develop ways to respond to problems when we know mostly that we may not be able to know with certainty. Ravetz (1986) calls this "usable ignorance."

The analysis is based on an ethnography of cooperation, conflict, and decision-making among scientists, shellfishermen, and bureaucrats. It is personal because my research, done between 1985 and 1988, was based on the participant-observation method, with heavy emphasis on participation. I was a leading participant in the genesis and implementation of the project. As a full participant, I was able to gain insights and perspectives otherwise difficult for an outsider to obtain but also thereby added my own predilections, blinders, and biases to the process and to this account.

THE PROBLEM: DECLINING HARD CLAM AND LITTLE APPLIED RESEARCH

The project's focus is the hard clam (*Mercenaria mercenaria*). Hard clams are distributed throughout the bays and tidal rivers of New Jersey, as are commercial and recreational clammers. Landings have declined since the 1940s.[2] Vast areas were closed to clamming because of pollution, particularly after 1961, and roughly 50% of New Jersey's waters are so closed (not all of this water is hard clam habitat). By the 1970s or 1980s, many of the open waters of the bays and tidal rivers of the state showed signs of serious to severe depletion of hard clams and overall landings had come to depend significantly on programs that allowed the relay of clams from polluted to clean waters. Participation in the fishery also has declined.[3] There is no question that many commercial clammers have quit because of declining catches.[4]

There is also little scientific data available to help assess and do something about hard clam population decline in New Jersey. The state's oyster industry, although now smaller in landings, revenue, and participation than the hard clam industry, has long received the bulk of research and enhancement efforts from both the state and the academic community. This may have something to do with the fact that it is located in one town, dominated by several large shucking and packing firms, and has a long history of organized political effort. The hard clam industry, in contrast, is comprised of thousands of independent harvesters, summer and weekend clammers, and dozens of scattered, independent dealers, and thus has less organized clout. However, knowing that the experienced scientists and technical resources needed to address the problem of hard clam decline exist, we used the spawner sanctuary program to bring them together. We sought to renew and create interest in hard clam enhancement studies, and, with the assistance of members of the industry and politicians, create a new impetus for estuarine shellfish research and development in New Jersey.

APPROACHES TO A SOLUTION: THE SPAWNER SANCTUARY PROJECT

The basis for our project seemed obvious: the need to restore the hard clam resource. The specific approach taken was a hard clam spawner transplant and sanctuary project. Clam spawner transplants originated in the bays of Long Island, New York, in the early 1960s, as attempts to increase the length of time that clam larvae were present in the bay (Kassner and Malouf 1982).[5] The "spawner sanctuary" is a refinement of this strategy, developed in the early 1980s by the State University of New York at Stony Brook (Carter et al. 1984) and implemented by two Long Island townships at Great South Bay. Clams are moved

[2]Landings are under-reported, perhaps by as much as fifty percent (T. McCloy, personal communication), making it risky to rely on these data for stock assessment. Clammers' accounts of changes in typical catches suggest, however, that the decline is real in most areas. Landings have stabilized in the latter 1980s. Official landings of hard clam meats in 1987 were 1.54 million pounds, with an ex-vessel value of 5.86 million dollars. Landings were slightly under the 1984 level of a little over 1.6 million pounds, but the ex-vessel value was higher than the $4.9 million of 1984. The use of clam meats as a measure of success is somewhat misleading for hard clams because the smallest clams, the littlenecks are worth the most, and clammers are almost always paid by the clam.

[3]From 1983 to 1987 the total number of licensed clammers, both commercial and recreational, declined 25%, from 20,550 to 15,280 (Bureau of Shellfisheries, unpublished data). The number of licensed commercial clammers was 2,875 in 1983 but only 1,935 in 1987, a 33 percent decrease.

[4]It could be argued that decline in the number of licensed clammers is due to improvements in the general economy, hence in alternatives to clamming. This is probably true, to some degree, in recent years as New Jersey's unemployment rate in the coastal counties has gone down to less than 4%. However, the parallel decline in licensed recreational clammers suggests that other factors play a role. Lack of adequate staff for enforcement of license requirements is one of those factors (G. Critchlow, personal communication). Poor catches is another. However, evidence is mostly anecdotal; catch per unit effort data are non-existent.

[5]The source suggests that baymen, rather than scientists, initiated the early transplants. I believe that the idea of spawner sanctuaries existed more widely and longer than suggested by Kassner and Malouf; New Jersey clammers and oystermen have long thought that the "chowders," for example, that they kept in protected coves or leases until the price improved had the beneficial effect, in the meantime, of increasing the amount of larvae in the waters.

from abundant to depleted waters and protected from harvest. The transplant increases the size of the breeding population. Their spawn may increase the chances of successful sets of hard clams in the depleted bays in which they are placed (COSMA 1985).

INCEPTION OF NEW JERSEY'S SPAWNER SANCTUARY PROGRAM

The idea of trying spawner sanctuaries in New Jersey was promoted by William P. ("Bill") Jenks, a clammer and bayman who found out about the Long Island spawner sanctuaries at a meeting in 1984 at which he gave a talk about another New Jersey hard clam program (Jenks and McCay 1984). He went with me to this meeting because I hoped to show scientists and administrators on Long Island that it is indeed possible to involve clammers in constructive meetings—my first stab at "co-management." I noted his reaction to such commingling: he left the meeting disgusted at the "objectivity" of scientists when men's lives are at stake, a not uncommon reaction of non-scientists to scientists, and one of the indicators of the sub-cultural differences that affected our project later. He also left the meeting intrigued by some things he learned, especially the idea of planting "chowder" clams in a protected area to repopulate the bays.

Elsewhere (McCay in press) I have described in greater detail how Bill Jenks and I worked together, with others, to stimulate interest in spawner sanctuaries in New Jersey. Bill read up on spawner sanctuaries and kept alive the idea of creating them in New Jersey. He persuaded me and others to take the idea seriously. He and I did the initial planning work in 1985. I knew how to write proposals and Bill knew a lot about clamming as well as enforcement and related issues. I prepared proposals to Sea Grant and to a new research and extension center in fisheries and aquaculture, referred to as the "Fish Tex Center," in which I billed this as an experiment in low cost"intermediate technology"[6] and in cooperative research and action. Cooperation and co-management were to be realized by having numerous co-principal investigators, including Jenks; a state biologist, Tom McCloy; a federal biologist Clyde MacKenzie; a marine extension agent, Gef Flimlin. They and several other people were willing to participate as long as I did the coordination and proposal-writing and Bill Jenks did the politicking. The proposals were for the planning process: determining whether and how to use "spawner sanctuaries" to help restore clam populations in depleted bays.

WHY CO-MANAGEMENT? THE EXPERIENCE OF THE HARD CLAM RELAY

The idea of using "co-management" as our vision of the spawner sanctuary project came from our experience with New Jersey's hard clam relay program. This program, begun in northern New Jersey in 1983,[7] involves the state-supervised harvest of clams from polluted waters and their transplantation to lots leased by the individual clammers in clean waters, where, within 30 days, the clams cleanse themselves of bacterial contaminants. I was impressed by the extent to which Bill and others managed the program, both publicly, in their participation in an advisory shellfish council, and privately, in close interaction with officials of the state's shellfisheries program. In a paper co-authored with Jenks (Jenks and McCay 1984; McCay 1985), we argued that the almost ritualistic hostility and allegations of favoritism between state officials and baymen that arose at advisory council meetings and in the press were generated by a management style in which the state developed its plans without involvement of those affected by them and then presented them to advisory councils or simply implemented them on the water. Formal involvement of a few respected baymen at an early stage of planning might have prevented some of the nastier episodes.

Moreover, the involvement of baymen in the management of the relay program was forced upon the state rather than encouraged by it. This worked against rational planning, reinforced an old legacy of cat-and-mouse games between clammers and enforcement officers on the bays and seas of the state, and tended to pit groups of baymen against each other, making it difficult for them to recognize and work upon their common interests. We suggested that the clammers should be officially and directly involved in the design and running of the relay:

> A general principle of planning in general and co-management in particular is to structure the process for maximal participation by those who are most directly affected by the program and thus have both the motivation and the experience to contribute to its effectiveness. People whose livelihoods are most at stake and who know the resource, environment, and industry from experience and trial-and-error experimentation are not only valuable sources of knowledge and advice but invaluable allies of the various branches of government involved in any complex management program [McCay 1985:8].

[6]Intermediate technology (Schumacher 1973) is an approach to development that questions the wisdom of capital-intensive, large-scale projects whose benefits are supposed to "trickle-down" to ordinary people; it poses instead the possibility of controlling the scale and factor-mix of technological change to be more appropriate to the resources and needs of the people who need "development" the most, i.e. the poor.

[7]The current program is based on one started in the early 1970s in southern New Jersey, near Atlantic City. Relays go back to the 1920s in New Jersey.

WHY AN ANTHROPOLOGIST?

There was more than serendipity behind the fact that the project was initiated by a clammer working with an anthropologist rather than with a biologist. My involvement was partly by default. State and university shellfish biologists were approached but none was willing to instigate the project (see McCay in press). Their responses were essentially the same as this, from a state biologist: "it's a good idea . . . but we have enough to do right now." No one but an anthropologist would help Bill Jenks. More than default was at work, though. The discipline of anthropology emphasizes respect for the people being studied and for the value of their knowledge. Hence an anthropologist is apt to take up the challenge to cooperate with someone like Bill Jenks.

In addition, anthropologists have a sub-discipline called applied anthropology, built on recognition of the value of not just studying people but also working with them to help them accomplish their objectives. Anthropology is also known for holism, an insistence on the interconnectedness of things and a willingness to account for rather than try to control away the complexity and diversity of human and natural communities. This may help explain why I remained with the project after its true complexity and difficulty revealed itself.

POLITICAL SUPPORT: FROM THE (EEL-)GRASSROOTS

An advantage to involving representatives of the user group, such as clammers, in a management project is that people at the grassroots are often smarter than academics about the need to obtain political support rather than rely on the goodwill and interest of state agencies or university scientists. The proposals were submitted in the summer of 1985. That summer Jenks appeared before the state's new Fisheries Development Commission to argue for its support of the hard clam industry and this proposal, and through his ability to gain the support of a coastal legislator, the spawner sanctuary concept became part of the recommendations of a legislative task force on the clam fisheries (Coastal Bay Clam Resources Task Force 1985).

We had little difficulty obtaining political support for the objective of planting hard clams in sanctuaries, especially compared with later trouble trying to gain support from the scientific community for research proposals designed to plan and evaluate the program. Contributing to our success in getting money to plant clams was the fact that the idea of transplanting shellfish and protecting them in sanctuaries to serve as a brood stock is very attractive public policy. It is simple and logical, understandable by almost anyone; and it is an example of something otherwise rare in common-property resource management: positive action instead of negative restraint.

CRISES IN CO-MANAGEMENT

Responses were much swifter than anticipated. By the early fall of 1985 the marine fisheries and shellfisheries group in New Jersey DEP's Division of Fish, Game, and Wildlife met with us and agreed to cooperate. We soon faced a crisis in co-management. In December 1985 state fisheries personnel began to design the project without including me or any of the clammers. We complained and regained central roles. In January 1986 an assistant commissioner of the DEP announced at a shellfish advisory council meeting that $10,000 would be provided for the purchase of clams for a spawner sanctuary for the spring of 1986.[8] A second crisis ensued over how that money would be spent. State biologists wanted to create a demonstration project with hatchery stock of the *notata* genetic variant of *Mercenaria* in Shark River, an enclosed and polluted estuary. The objective was to see whether a spawner sanctuary could work so that we could go to the legislature for more funds with proof in hand. However, Bill Jenks, the clammer who started the project, was upset at what he saw as misuse of scarce funds. Even though he and I had noted the possibility of using *notata* clams as a marker, he insisted that the Shark River project was a misuse of the funds. They should be used, instead, for a bona fide spawner sanctuary in open waters so that clammers could take direct advantage of the results.

For my part, I was upset that decisions about the spawner sanctuaries were still being made only by state personnel when the proposal called for planning that involved not only other shellfish scientists in the region but also baymen. After many phone calls and some politicking (including phone calls to state officials from legislators), the state agreed that the money would be used for a true spawner sanctuary, in clean and open waters, and that our original intent, of using the best possible scientific minds to advise us, would be followed.

The outcome was that there was no money for planning, just for implementing a sanctuary. Subsequently we obtained additional funding from a variety of sources,[9] most also earmarked for actual implementation of sanctuaries. But we had to plan for the immediate reality: planting clams in a spawner sanctuary in May 1986.

APPROACHES TO THE PROBLEM OF UNCERTAINTY AND IGNORANCE

By early January 1986 we knew that $10,000 was available to begin planting clams that spring. We had to abandon the idea of rational planning for the project and to

[8]Her announcement was evidently part of an attempt to ward off mounting criticism from clammers who were dissatisfied with what they saw as little attention paid to their concerns. She accepted a challenge to attend a shellfish council meeting and brought as her gift this announcement.

[9]Sources of funding included the New Jersey DEP Bureau of Shellfisheries, the New Jersey Fisheries Development Commission, the Fish Tex Center at Rutgers University (Fisheries and Aquaculture Technology Extension Center), Ocean County Board of Freeholders, the New Jersey Agricultural Experiment Station, and the federal Coastal Zone Management Program. Legislative bills for additional funding lapsed in the legislative process.

take on a more incrementalist approach, in which major questions about goals, objectives, and methods were set aside as decisions about more immediate matters were made (see Lindblom 1969, 1979). We muddled through, and as we did some of those goals and methods emerged and many mistakes were made and lessons learned, as expected from incrementalist theory (ibid).

Not only did we lack the time and resources to engage in rational planning, but we were confronted with a situation of radical scientific uncertainty and even ignorance. Very little research on hard clams and on the relevant aspects of the ecology of their environments has been done in New Jersey in recent decades (but see Kennish and Lutz 1984; else one must go to Carriker 1961). We clearly did not have the data available to use a larval dispersion model for siting spawner sanctuaries comparable to that used, to some extent, in Long Island waters (see Carter et al. 1984).

Our approach to the problem of decision-making in a context of scientific uncertainty and ignorance became evident as we went along. It was to be very humble about what might be accomplished and to take advantage of the best available scientific advice, combined with information from baymen, in making decisions. It was also to be willing to act on the basis of very little scientific information.

I was influenced by a conversation in January 1986 with one of the shellfish biologists in New York State who had been involved in studies related to hard clam and bay scallop spawner sanctuary projects in Great South Bay, Long Island. A great deal of money had been spent to do a hydrographic model of Great South Bay, and in turn to use it to determine where to plant spawner stock in relation to patches of phytoplankton distribution and the movement of larvae. He observed that all a model such as this does is "teach us what we don't know." Moreover, given vigorous debates in ecology about equilibria vs. stochastic processes in nature, it is difficult to take a predictive model seriously. I used his observations to justify our beginning the project without hundreds of thousands of dollars worth of basic research into the physics, chemistry, and biology of the bays.

We felt that starting off with a spawner sanctuary program would help delineate and stimulate scientific research appropriate to the questions that arise from that program rather than broad-brushed and expensive large-scale studies. We also felt that this program would help initiate the restoration of applied hard clam research in New Jersey. Indeed, an important outcome of the project would be the creation of a position in applied hard clam biology, occupied by Stephen Fegley as of July 1987. From the outset and many times thereafter, we said publicly and in private that the goal of the project was hard clam enhancement, whatever that takes. We assumed that reaching this goal requires a strong applied research program in hard clam biology and management as well as genuine public commitment to the shellfisheries, and that the hard clam spawner sanctuary project should be seen in this light.

Our inclination to act without a substantial body of data began early in the project. Clyde MacKenzie, a NMFS shellfish biologist, agreed to help me and Bill Jenks with the project. He approached it with this attitude: "it sounds like a good idea; so let's do it!" When I first heard him say this, in the autumn of 1985, it was disarming; I had just written a long proposal for a year of feasibility study and planning. But it was heartwarming to Bill Jenks and other clammers, who distrust anyone who "just does a study." MacKenzie's attitude and approach turned out to be typical of the people most influential in this project. Clyde MacKenzie has worked with members of the oyster and clam industry for many decades, often on projects as applied as this (see, e.g., MacKenzie 1975, 1977, 1983) and is committed to "managing for abundance" by controlling predators and other interventions in nature (MacKenzie 1979). He is inclined more to *praxis* than to theory, and believes that clammers have much to teach biologists.

Mackenzie's attitude, the baymen's inclination to distrust scientists and feasibility studies, and the unexpected receipt of money from the state led us to accept a major change in tactic: action first, science later. The idea became to start something and trust that this would attract the scientists and science required. As the marine extension agent, Gef Flimlin, said to a reporter, "what we're doing is a whole new concept in that we're doing it first and they're studying it later. We're taking the first step, creating the situation for them to take and study" (*Ocean County Observer* May 11, 1986).

"Action now, science later" was reinforced by other participants in the process. Although some biologists who participated in our planning meetings emphasized the need for more information before planting clams, Harold Haskin, one of the most respected shellfish experts, suggested that we knew enough already, as shown in this segment of a discussion of the problems in evaluating a spawner sanctuary.

> McCay: "Do you think a Spawner Sanctuary would make any difference then?" Haskin: "Well, it can't hurt. I'm all for it because the more parents you've got in an area the greater the probability that you're going to get some sets. You can't go wrong on that." McCay: "You accept that it's an unpredictable system but you're hoping to increase the odds." H: "You're increasing the odds, . . ." (Transcript, 1/27/88 meeting)

We therefore put the proverbial cart before the horse by initiating a spawner sanctuary program in New Jersey, but by so doing we helped to redress the problem of little scientific data.

BAYMEN AND SCIENTISTS AS DECISION-MAKERS: SITE SELECTION

In the meantime, decisions about how to run the spawner sanctuary program had to be made. We used two

approaches. The first was to tap the knowledge and experience of baymen. Bill Jenks provided 113 items of advice and information based on his experience and observations. Bill and I also interviewed baymen and invited some to decision-making meetings. The second was to do the same for shellfish biologists and state administrators.

One of the arguments for co-management is that the users of a common-property resource are likely to have information and perspectives valuable to management. With inspiration from MacKenzie and from biologists like Johannes (1981) who emphasize the importance of the biological knowledge and lore of users of the marine environment, Jenks and I carried out a fact-finding expedition. In August and September of 1985 we spent three days talking to clammers, clam dealers, and aquaculturists about conditions on the bays, the concept of spawner sanctuaries, and, using charts and an ingenious system developed by Bill, where spawner sanctuaries should be located. Their responses to our questions about sites (both to plant clams and for settlement of larvae) were recorded with a straight pin on the chart; on the back of the chart each pinprick was linked to an informant, but otherwise the informants could not easily see sites chosen by others.

Our goals were several. One was to test the waters, as it were, in New Jersey coastal areas outside Bill's normal range, to see if we could count on support from very powerful clammers and oystermen there. A second was to publicize the project and generate general interest. The third goal was to use the experience and knowledge of clammers as much as possible in the project. This information would become part of the basis for making decisions about siting and other aspects of the project.

At a meeting of shellfish biologists, clammers, and state biologists and administrators on January 17, 1986 the scientists who came—six, from New Jersey and New York—reviewed the results of our survey. Jenks put our charts on the wall, showed where the pin-pricks were and revealed some of the comments made by those we interviewed. He noted criteria that should be used, in addition to those prompted by hard clam biology, in site selection, foremost among which is the need to protect the clams from poachers. Combining our findings with the biologists' own knowledge of the bays in question or similar bodies of water, we selected and ranked the more promising sites. Bill Jenks reported on what he observed and what the clammers he and I interviewed said, and scientists such as Harold Haskin and Bob Loveland of Rutgers and Bob Cerrato of State University of New York at Stony Brook discussed specific sites as well as the spawner sanctuary in general.

For example, Bill reported that a former clam dealer in Barnegat Bay recommended not planting there because of the effects of the partial closure of an inlet:

> Now, Stan Cottrell says, at this time, in Waretown there is a tide rise of only six inches and that was eighteen inches just fifteen, twenty years ago, so due to the inlet's closure or partial closure this is affected . . . In his words, he said, 'I wouldn't plant a clam in Barnegat Bay, I would go for Little Egg [Harbor] and Great Bay.' Now there's a man that lives right on the bay and was the biggest dealer in the area [Jenks, transcript 1/27/88]

Dr. Haskin responded that he and his colleagues had come to the same conclusion a long time ago, based on plantings of clams in locations from the lower end of the Delaware Bay on up to Raritan Bay:

> . . . and as I understand—this was in the late 40s and early 50s—there seemed to be an inverse relationship between the growth rate of clams and the density of clams. That's where you had your heaviest populations you also had your smallest growth rate, and . . . looking at the food conditions and what have you, we decided that it wasn't just a matter of a large population having enough food but it was rather a question of the current system. Where you've got currents that are rapid enough to . . . provide a lot of food you also were losing most of your larvae because you were tearing them out to sea with a strong tide [Haskin, transcript 1/27/88].

Accordingly, Haskin too recommended Little Egg Harbor over Barnegat Bay: ". . . Little Egg Harbor was an area which in those days had an awful lot of clams and it doesn't have a big flushing rate so that I think, just on a kind of general target area, . . . I'd look pretty closely at Little Egg" (Ibid).

Ironically, Barnegat Bay was the location of one of the sites chosen, despite recommendations of clam dealers and scientists. The sites we used—one near the town of Barnegat in the southern end of Barnegat Bay and the other in Parker Cove, Little Egg Harbor—were finally chosen after a tour of prospective sites with a member of the marine enforcement unit. Both met these criteria:

1. areas once known to have been very productive but in recent years not so;
2. deep enough to discourage treaders; and
3. close enough to roads and docks to be relatively easily monitored by enforcement officers. This consideration appeared to have been enough to rule out every alternative site except the lower Barnegat Bay one.

In retrospect, neither site was appropriate. The one chosen solely for law enforcement reasons, the Barnegat site, may have been the worst choice for the same reason, given high levels of illegal clamming in that area. The one chosen because of what seemed to be superior conditions of circulation, etc., the Little Egg Harbor site, may no longer have good environmental conditions for clam reproduction. But we probably would not have known these and other problems if we had not committed ourselves to action. Errors such as this that we made by muddling through were

costly but, one can argue, irreplaceable learning experiences.

OTHER MATTERS DISCUSSED AT THE JANUARY 17, 1988 MEETING

Similar interchange among scientists, baymen, clam dealers, and state fisheries, water quality, and enforcement personnel took place on other topics. For example, Dave Vaughn, a shellfish biologist then working for a hard clam mariculture hatchery, talked at length on the topic of the complexities of hard clam spawning behavior in different bays and the importance of timing a sanctuary transplant in relation to this. Others talked about evaluating whether a spawner sanctuary works, possible genetic techniques, and effects of predators on resulting clam seed.

The day-long meeting was also devoted to discussions over the details of actually getting, moving, planting, and protecting clams, including discussions of bidding, what kinds of gear could be used and by whom, the price of clams, how the clams would be painted and by whom, how clams from condemned waters would be monitored to ensure that they made it to the planting sites rather than consumers, and so forth. The meeting itself was a remarkable event, the first time in many years that so many shellfish scientists from different institutions, academic and government, and so many state administrators, and baymen and shellfish dealers, came together (voluntarily and without compensation beyond clam chowder, as we had no money at this point) to cooperate in planning something.

THE TRANSPLANT: TROUBLE AMONG THE RARITAN BAY CLAMMERS

As a result of the January 17, 1986 meeting and several others as well as many telephone calls, we planned the first New Jersey hard clam spawner sanctuary. Following the lessons learned in Long Island, we intended to buy only large chowders, of low market value and thus both inexpensive to purchase and less likely to be stolen from the sanctuaries, and to paint them, again to remove some of their attraction to poachers. Aware of past hostility to proposals to transplant clams from Raritan Bay, we decided that this project should involve the fishermen of the Raritan Bay area as much as possible, including paying them to harvest clams. The clammers would store the clams in trucks with locks approved by the marine enforcement unit, and after enough were accumulated the clams would be trucked to the dock at Parker Cove, LEH, the site of the first sanctuary. The state agreed to survey and stake off the site and to provide necessary enforcement manpower.

The spawner sanctuary did not work quite this way. One of the lessons we learned was not to overestimate the ability of the clammers involved to handle issues of equity and competition amongst themselves, and at the same time not to overestimate the ability of the state to make decisions that affected such issues. At first we thought that we could arrange for the harvest of clams informally, by letting out the word that we were interested and waiting for potential clammers to get in touch with us. Referring to a Jersey shore town that was once the center of clamming, Bill called the process "relying on the Tuckerton teletype" or gossip network. By this process we made arrangements with a crew from the community of Belford, on Raritan Bay, who participated in our January 17, 1986 meeting. Very soon thereafter we received angry phone calls from other fisherman in that community and clammers and dealers elsewhere who forced us to "go out for bids," through an elaborate, time-consuming bureaucratic process.

No one bid (clammers later told us that the procedure was too formidable, but fishing and lobstering were also good that season), and thus we relied on the original crew, a trio of older fisherman all of whom had experience in clamming in Raritan Bay that predated the 1961 closure of the bay because of pollution. However, they in turn refused to clam for the project.

The crew had gone to the expense and trouble of making a special dredge. We obtained for them all the permits required for them to be allowed to dredge for clams in polluted waters. They went out to get clams one day in April, with a marine enforcement officer on board, and came back with nothing. They went out again, returning again with nothing and determined to quit. They felt they had been misled about the waters open to them and could not catch enough in them to make it worth their while.

The Belford crew pressured us to get regulations changed to open other Raritan Bay waters to them. This placed us in a terrible bind. The beds they wanted to dredge were in an area marked on the official chart as available to participants in the state's hard clam relay and depuration program. The men who work in that program use tongs and rakes, not dredges (which are illegal in New Jersey's clam fisheries). The Belford men with whom we contracted had special permission to use a mechanical dredge from a large vessel. The relay and depuration clammers were angry about Belford fishermen dredging in 'their" waters. They let us know through phone calls and rumor of a petition or even law-suit. To make matters worse, Bill Jenks, the representative of clammers on our project, was a relay clammer and so too his sons, and thus could not allow anything that would offend the relay clammers. The state shellfisheries officials, recognizing a familiar political storm brewing, refused to make any of the changes demanded by the Belford clammers. We were stalemated.

Although Bill Jenks and I, from our separate experiences, he as a clammer and shellfish enforcement officer for some years, I as an anthropologist, felt we knew the people of the area well enough to be able to hire a crew to

catch clams, we failed.[10] Cooperation, experience, sensitivity to social and cultural differences, all of these may not be enough.

We then turned to the relay and depuration clammers who worked out of the community of Highlands, hoping that if the chowders were thick in "their" area of Raritan Bay, as the Belford men said they were, we could get them —more slowly and with more logistical problems—from tongers and rakers. Phone calls, meetings with the owner of a clam depuration plant in Highlands, meetings and calls with state water quality and shellfisheries officials, led to nothing. Regulations for the relay and depuration program forbade the direct sale of clams to anyone for any purpose. None of the state officials involved in the project was willing to go to the trouble required to get the regulation changed.

Our underestimation of the effects of long-term factionalism within the shellfisheries of the region and our overestimation of the willingness or ability of state "co-managers" to cooperate led to weeks of fruitless negotiating. Finally, we changed our plans. Clams had to be planted soon. The state money had to be spent by October, and we wanted to give the transplanted clams a chance to spawn in their new home before summer began. So we were forced to engage in what at times seemed both the sublime and the ridiculous: buying from dealers chowder clams, many of which came from the same bay into which we would plant them. It was, however, suggested that creating a dense aggregation of clams into one area might help induce spawning and a higher rate of fertilization of eggs. Then we misjudged the chowder market. We expected that local dealers would be interested in selling chowders to us because of a traditionally poor market for clams in late spring. In fact we had difficulty obtaining enough chowders for our sanctuaries. This was, we were told by one of the dealers, partly because we were competing with the managers of the Long Island spawner sanctuaries for New Jersey chowder clams. Knowledge of this helped restore at least my faith in the project: we were paying clammers to keep local chowders in the bay!

CREATION OF THE 1986 SPAWNER SANCTUARIES

Finally, in May and June and then October, 1986, we bought, painted and then dropped overboard 218,700 hard clams into the two "spawner sanctuary" sites in Barnegat and Little Egg Harbor bays. Biologists in the state's Bureau of Shellfisheries surveyed and staked the sites and, with the state's Division of Water Resources (all within DEP) had them formally designated as "condemned" waters. Clams for the Parker Cove site came from local dealers. Some of the clams for the Barnegat site came from clammers who harvested, under special permit, clams from condemned waters in Raritan Bay. We paid clammers and dealers for the clams at roughly the local market rate.

The clams were painted red with rollers on an ingenious rack by groups of county prisoners on a work-release program. The paint was to discourage poaching. It was chosen to minimize known toxic hazards while providing acceptable drying speeds. The clams were spread over one-acre plots within five-acre lots that had been surveyed, staked, and designated as sanctuaries. The sanctuaries are classified as polluted waters by the state so that theft of the clams is a very serious offense. We paid local clammers to spread the clams for us. At a later phase of the project, some of the Raritan Bay clams were painted yellow and planted in the Barnegat sanctuary in discrete areas for ease of discrimination in future research.

In the fall of 1986 we were able to return to our original plan. We found a pair of young clammers who were willing to dredge clams at our price in Raritan Bay and, most important, to paint them on board, allowing them more flexibility in the timing of their deliveries to the planting site and reducing our hassles in painting the clams. They received a special permit, through our program, to dredge clams in highly polluted waters just for the spawner sanctuary. Marine enforcement officers had to watch them carefully. Because they had never dredged for clams before their level of production was low and erratic. So we also set up two days of buying clams from dealers and using the prisoners to paint them.

CO-MANAGERS AND CO-MANAGEMENT

The spawner sanctuary program has been full of administrative and socio-economic challenges. Among these are finding ways to fairly compensate and coordinate the activities of the harvesters and transplanters and to deal with competition among different interest groups, coordinating the research activities of the scientists involved, searching for funding for the purchase of clams for the sanctuaries, and sustaining the notion that industry, academia, and state and federal governments can indeed cooperate.

Many of these tasks were done by a small team. In January 1986 Gale Critchlow, Chief of the Bureau of Shellfisheries, and I agreed to be official co-directors of the project. She called upon other state personnel as necessary and helped create and maintain public commitment to and minimize bureaucratic interference with the program. I managed the money, planned and held meetings, wrote up bid specifications, and spent many hours on the telephone

[10]There may have been more at issue in our difficulty in getting Raritan Bay clammers to work for the project, including their enduring suspicion of any program designed to move "their clams" from local waters to other waters. This harkens to an ancient "north/south" conflict among shellfishermen in New Jersey, but also bespeaks continuing bitterness over the failure of the state to do anything to help the large numbers of clammers forced out of business when pollution resulted in closure of most shellfish beds in northern New Jersey in 1961.

with Gale, Bill Jenks, Clyde MacKenzie, and others on the project, working on the details and general approach.

The participants in the program, besides biologists and other scientists who attended planning meetings and helped define new research agendas, comprised a number of state officials with direct mandates concerning shellfish and water quality and a more motley band of assorted scientists, clammers, and administrators. The success of the project depended very much on the nature and talents of the individuals involved, particularly those who were able to bridge social boundaries, to work in more than one cultural world.

PROBLEMS WITH THE STATE

The state officials involved in the project showed enthusiasm and willingness to cooperate in the early phases, and Gale Critchlow continued support for it into a second year of funding from DEP. Elsewhere (McCay in press) I describe her and others in the state, emphasizing the extent to which they shared qualities observed in other key actors in this experiment in co-management, especially the ability to work closely with people in other roles. I also there note the emergence of a disturbing distinction between "the real workers" and, by default, the state participants in the program.

The state personnel avoided any direct involvement in the project beyond helping with regulations and, at first, putting up stakes. We needed help. For example, who was to plant the clams on the site? State personnel claimed not to have the boat or time to do the work, but on the first day of planting two state biologists showed up with a new, very substantial boat, and stood around observing the work and the attention we were getting from the press, while a clammer we hired to plant the clams went back and forth with bags of painted clams in his tiny clam boat. That was a major source of aggravation to other cooperators, as was the more pervasive "no-show" response of state personnel who had otherwise pledged themselves to the project.

Among the important problems we experienced were:

1. getting rapid action on critical matters (i.e. permits), a problem understandable given busy schedules and normal inter-agency fragmentation and administrative and legal complexities; and
2. the "no-show" problem alluded to above, a social relations gaff that reinforced perceptions of strong social boundaries and subcultural differences between "the state" and others.

In addition, despite great concern over the fate of clams transplanted from condemned waters of Raritan Bay, supervision of that transplant was negligible, a fact that may have contributed to our later difficulty finding any Raritan Bay clams in the Barnegat sanctuary. Further, the state participants in the project continued to aggravate the others in 1987 and again in 1988 by their failure to act rapidly to re-stake the sanctuary sites after ice, baymen, or other conditions destroyed the stakes.

As understandable and defensible as they or the delays in changing them are, state rules and regulations and personnel and budget limitations were viewed by the non-state co-managers as troublesome every step of the way. The people involved tried to minimize the damage and to cooperate when they could, but the definition of "when they could" was probably different for them than for other participants in the project. Among features of their bureaucratic situation that appear to have constrained their ability to cooperate was the tendency of individuals working for the state to minimize any action that will cause a reaction. It was put this way, in a different context, by one of the state employees: "I didn't want to aggravate them because they would just turn around and aggravate me."

However, Gale Critchlow, co-director of the project, continued her interest in and commitment to it. It had the potential of being one of the few positive things she, as a regulator, could do for the shellfish industry. She found $10,000 for another spawner sanctuary, and she successfully brought in a federal coastal resources grant for another $20,000 in 1987.

THE "REAL WORKERS"

The stalwart band of workers found with bags of clams and cans of red paint on the docks of Parkertown or Barnegat, New Jersey, in May and June 1986 comprised a retired clammer and his wife (Bill and Vivian Jenks), a marine extension agent (Gef Flimlin), the assistant director of the Fisheries Development Commission (Hal Bickings, Jr.), and from time to time an anthropologist (McCay). They were joined by a group of prisoners from a county jail and their warden, Officer Jim Davis. On an experimental work-release program, the prisoners did the actual painting and helped out with jobs like bagging and hauling bags of clams for planting. There were others, i.e. clammers who planted the bags of clams for us in the designated "sanctuary," and dealers who made special efforts to fill our needs when they had other markets for "chowders." My department secretary did her best to make sure the dealers were paid. We were a media event, celebrated in one newspaper heading as "Convicts and Clams," and as such attracted local and state politicians who gave press conferences at our planting sites.

The people who consistently showed up at the painting/planting sites, the "real workers," almost all shared practical, action-oriented approaches to problems. The scientists and state administrators who from time to time "really worked" are unusual in their commitment to "grassroots" approaches to problems. They and the clammers and others who worked on this project had special skills in bridging boundaries between scientists and industry, which are described elsewhere (McCay, in press). Most, like Jenks, are politically savvy, experienced on the water, respectful of

the knowledge of both scientists and baymen, and inclined to action.

EVALUATION

Unmet Goals and Responses

These are some of our disappointments and how we are dealing with them:

1. We were unable to carry out the original plan of using clams from polluted waters in Raritan Bay to help restore productivity elsewhere. Factionalism, based on real differences in situation among different groups of clammers, made this next to impossible. More generally, the clamming industry's enthusiasm and support for the project faded rapidly after the early phase of it, and by late 1986 even south Jersey clammers were publicly expressing skepticism about the project.

   If more clammers from different regions and segments of the industry had been involved from the start, their support might have been more enduring. Accordingly, in 1987 we designed the composition of a new Hard Clam Research Committee of the Fisheries Development Commission to have broader representation. Another possible factor was the improvement of clamming in the bays to the south of our target area which reduced perception of the need for the project. In addition, clammers, like scientists, are skeptical although hopeful about interventions in nature such as this.
2. The clams we transplanted did not seem to fare very well. Those planted at the Barnegat site, both from Raritan Bay and from local dealers, seemed scarce not long after planting (Fegley, personal communication). Clams may have dug deep (MacKenzie, personal communication). Some participants feel that few of the clams were actually planted (because of lack of enforcement at that end during the Raritan Bay transplant) or that poaching took place soon after the planting.

   It was difficult to communicate the idea of "co-management," especially with its implication of shared responsibility, to members of the clam industry. Clammers and dealers were inclined to see this as a state project. The state is perceived either as a meddling bureaucracy or as an abstract source of largess. Whichever, putting hundreds of thousands of clams in a small area of the bay, then labeling them Property of the State of New Jersey, is tantamount to saying, "here they are, come and poach 'em." This was worsened by the difficulty we had persuading the state to keep the sites staked.[11] Because of the poaching problem, the Long Island spawner sanctuaries have been redesigned as small, scattered plantings without visible markers (Kassner, personal communication), and our new, small-scale experimental ones are being done the same way (Fegley, personal communication).

   Many of the clams planted at the Parker Cove site, in Little Egg Harbor, appear to have stayed there, but their health was poor. I obtained funds from the Fisheries Development Commission for analyses of fecundity and survivorship of planted clams in comparison to native clams. Between May and October 1987 Steve Fegley and Bruce Barber collected spawner clams, and found that survival during the first year (estimated at 73%) was lower than what could be expected by more careful handling and placement. More seriously, they found that gamete production was suppressed in Parker Cove clams, suggesting that environmental or nutritional conditions are not favorable for clams there (Barber et al 1988). It is possible although still not proven that environmental changes caused the scarcity of clams in Parker Cove that led us to select this as a site, and those same environmental conditions make it a poor place for clam spawner sanctuaries.

   Attempts to evaluate the first major spawner sanctuaries continue. Moreover, Fegley has begun to develop small spawner sanctuary experiments with some controls and to focus on the critical question of what happens to juvenile hard clams in the wild.
3. An outcome of one of our meetings was the idea of exploring whether genetic differences between clams from different areas would be useful as a way of evaluating whether a spawner sanctuary works. Beyond chronological coincidence—a set following the planting of clams—there is no known way to accurately determine whether a spawner sanctuary increases the likelihood of a set. We persuaded the evolutionary geneticist Robert Vrijenhoek and his student to investigate the potential of using genetic variability to distinguish clams. This seemed appropriate at the outset of the project, when we still believed that we would be able to obtain most of our spawners from Raritan Bay. Raritan Bay and the planting site in Little Egg Harbor are over seventy miles, and many other obstacles, apart. If we planted Raritan Bay clams in Little Egg Harbor then when a new set occurred it may be possible to distinguish descendants of Raritan Bay clams from descendants of native clams. Sadly, genetic discrimination techniques have revealed no geography-based variability (Vrijenhoek, personal communication).[12]

[11] Lack of proper staking is yet another sign that the state is bumbling, and hence to be taken advantage of. It is also a signal that poaching is all right because even if caught, one would not be convicted for want of evidence.

[12] Geographic isolation is probably more the exception than the rule. When we began negotiating with Vrijenhoek to research the possibility of ge-

4. Our hopes for a scientific breakthrough in techniques for evaluating a spawner sanctuary were dashed. More seriously, however, it seems that participants in the project, particularly the scientists (including peer reviewers of proposals), came rapidly to the conclusion that creating spawner sanctuaries was not worthwhile. The lack of a technique for measuring their effectiveness was a major reason. There are other reasons for being skeptical about hard clam spawner sanctuaries, and certainly about specific sites. This one, however, seems to reflect our tendency to confuse technique with truth: if I can't measure it, then it is not there.

   Accordingly, we were unable to obtain funding from the Office of Sea Grant, a federal government agency for scientific research related to the objectives of the spawner sanctuary project. I received a small amount for administration and analysis of the project, but our attempts to put together a truly multi-disciplinary, multi-institutional problem-focused research program did not make it through peer review and Sea Grant muster. This partly reflected widespread skepticism in the scientific community about hard clam spawner sanctuaries. The project is barely kept going by small grants from the Fisheries Development Commission and the DEP and support for Fegley from the Fish Tex Center.

DEALING WITH SCIENTIFIC UNCERTAINTY

Three summary points can be made about New Jersey's hard clam spawner sanctuary project. First, whether by design or happenstance, it was an example of the style of decision-making known as incrementalism, or "muddling through" (Lindblom 1969). Our policy of "action first, science later" was an example of incrementalism, as opposed to a "rational-comprehensive" approach to decision-making in which decisions and actions are based on complete and scientifically valid comparisons of all alternatives with reference to predetermined goals. We had little choice: our funding was for planting clams, and the information based required for a rational-comprehensive approach was not available to us. However, by basing our decisions on the advice of scientists working from very limited data, we were able to establish a program. We "muddled through" without clear ideas of exactly what we wished to accomplish or how we would do it, just trying at the outset to get something going, and then forced to hurriedly plan a spawner sanctuary. Nonetheless, as Lindblom (1969, 1979) would predict, we were thereby able to stimulate consideration of both goals and means of achieving them that will enable a more rational approach or at least better-informed incrementalism in the future.

Second, co-management worked, at least to the point of creating two hard clam spawner sanctuaries, largely because of the strong commitment of a handful of people who were willing to try to communicate across social boundaries with the goal of getting something done. Distinctions between "ordinary knowledge" and "scientific knowledge" and the ways people perceive these forms of understanding are essential to understanding the difficulties that lay people and scientists have in working together. It may be that, as Lindblom and Cohen (1979) have suggested, we must ask about "usable knowledge." The people who made this project work are those who were able to cast scientific knowledge not only into ordinary language but also into the practical concerns of ordinary people; they are people who, whether scientist or bureaucrat or clammer, seemed to care little about competing claims for legitimacy but instead to be most concerned about what the social scientists call "praxis" or "social action," and what others might describe as "getting something done." However, the perceptions the activists held of those who were more cautious or participated less overtly contributed to the social fracture points of this experiment in cooperation (see McCay in press).

Third, the project was disappointing in terms of the goal of a sustained and co-managed spawner sanctuary program in New Jersey. The cooperative, multi-disciplinary team of 1986–87 was by 1988 truncated to a small handful of people, and no more large spawner sanctuaries were planned. One reason was increasing awareness of high levels of uncertainty and risk about hard clam spawner sanctuaries, which led to skepticism about the project.

The project is fraught with skepticism and uncertainty, indeed with ignorance. As the philosopher of science J. R. Ravetz recently argued (1986), the world is increasingly faced with ecological and social problems with which science is hard pressed to deal because there is so little known about them. Scientists are very uncomfortable dealing with questions such as "What's going to happen to the biosphere," and especially with answers such as "We don't have any way to know." He offers the concept of "usable ignorance," as an adjunct to "usable knowledge." Scientists increasingly must be able to interact with others, of different disciplines, and of different professional and social backgrounds, to adequately cope with ignorance and in so doing make it useful. They must also be able to appreciate the points of views of others, which include different criteria of quality and truth.

The hard clam spawner sanctuary project—and the larger questions of what causes variation in hard clam abundance and what can be done to affect that—are apt examples of the kinds of problems to which Ravetz refers.

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netic markers in hard clams, Bill Jenks wrote down the occasions he knew of since ca. 1950 when large quantities of clams were moved by clammers from one bay to another in New Jersey. In particular, a few explosive sets of hard clams, when beds were dense with small juveniles, led clammers and dealers to gather great quantities of undersized clams and plant them in leases elsewhere or sell them to others in and out-of-state.

Very little is known, and what we have found so far is that we don't (yet) have a way to know, for sure. Transplanting "spawners" to increase clam production is not proven to be effective. As noted earlier, methods have not yet been found to evaluate spawner sanctuaries, i.e., to distinguish the offspring of the transplanted spawners from the offspring of native clams. Moreover, the project rests upon several unproven and questionable assumptions, including (a) that one could ever realistically plant enough clams in a large estuary or bay to make a measurable difference (Kassner and Malouf 1982); (b) that the number of spawning clams in one generation affects the numbers of survivors of the next generation (the stock/recruitment relationship); and (c) that decline of clams in an area is due to depletion of spawning stock rather than environmental changes, Fegley, personal communication), changes in the intensity of predation (MacKenzie, personal communication), or other factors affecting clam reproduction and survivorship.

Our recognition of the nature and extent of the problem of decision-making given scientific uncertainty and ignorance developed with the project, as did our approach to it. It was to be very humble about what might be accomplished, to take advantage of the best available scientific advice, to recognize that baymen, too, might have "usable knowledge," and to hope that starting off with a spawner sanctuary program would help delineate and stimulate applied scientific research on hard clams.

I have used terms such as "our approach" in this article, but do not mean that every one involved in New Jersey's hard clam spawner sanctuary project was aware of or in agreement with what I said. A multi-disciplinary, co-operative project such as this involves negotiation among many, sometimes conflicting, approaches. Clark and Majone (1985) identify five major roles in policy-relevant science: scientist, peer group, program manager or sponsor, policymaker, and public interest groups. They identify differences in what they do, the questions they ask and criteria and processes by which they choose and make decisions. In this case, the critical roles are somewhat different: academic scientist, government (applied) scientist, peer group (in reference to proposal review), program manager, government regulators, public interest group (the clammers). The approaches we took to the problem of uncertainty and ignorance arose out of competition and tension among the approaches of representatives of those groups.

For example, clammers who participated and were interviewed did their best to simplify the problem and solution: "we need action now." They also were very skeptical about the value of scientific research and suspicious if not hostile to any move that would place scientific research before practical action.

As regulators, officials and employees of DEP were concerned about law enforcement more than science. For example, the siting of the spawner transplants would be determined as much by relative ease in watching the sites from a patrol car as by suitability for clam spawning and larval circulation. As government agents, they were also concerned about political ramifications of the project. Because of the tremendous political support garnered by Bill Jenks,—and the inherent appeal of the project—state officials such as Gale Critchlow, Chief of Shellfisheries, gave us enthusiastic support. But her concern, and the concern of most others in the state, was to find out whether it worked as quickly as possible so that they could have evidence to use in asking legislators to appropriate more money for the project. Hence, the emphasis was on quick-and-dirty science, but uncertainty and ignorance about whether the spawner sanctuary worked was unacceptable. There had to be answers. Once they found out there were no quick answers, they tended to lose interest. The politicians involved shared that perspective to some extent, but also tended to support whatever their constituents, i.e., the clammers, wanted.

The role of scientist must be more precisely delineated. The academic scientists concerned about data quality, validation, and such as well as professional recognition maintained strong pessimism and emphasized the need to find ways to evaluate spawner sanctuaries, such as genetic discrimination. Their peers reinforced those messages in evaluating proposals for research support. The biologist Fegley's major task is to satisfy the skeptics by determining whether spawner sanctuaries can work, and he is engaged in controlled experimentation to this end, but he must do so in a way that will enhance his credentials as a scientist.

Government scientists by and large have different peers and pressures. Bureaucratized scientists, who must deal with limited budgets and many and conflicting demands from the public and policy-makers, share many concerns and ideals with academic scientists, but they are strongly concerned to minimize involvement in new projects of any kind and to cover their flanks against possible challenges from the public and politicians.[13] In this case, state shellfish biologists said they were too busy to be actively engaged in the project, although they eventually did essential tasks such as surveying and staking out the sanctuary sites and they came to our numerous meetings.

But there are applied scientists who work for government but are more insulated from the public and policymakers as well as much of the professional system of the academics. They have more freedom to explore new projects fraught with scientific uncertainty. Our example

[13]Moreover, possibly because many of the government biologists work for regulatory agencies and are therefore often in antagonistic relationships with clammers, they tend to denigrate the value of the clammers' knowledge and experience. The clammers are the ones who are raping the resource, and the biologists have the lonely, often thankless, role of trying to protect the resource for long-term and public interest.

of this type was Clyde MacKenzie, of the National Marine Fisheries Service, who from the outset took a very optimistic stance about spawner sanctuaries and engaged in small-scale, very practical research, much of it on his own, during and after the transplants.

There are also applied scientists from academia who by virtue of position or stature in the profession are also more willing to offer advice and make decisions even when there is a great deal of uncertainty and ignorance about the facts. Harold Haskin, Professor Emeritus of Oyster Culture at Rutgers University, is an example of the latter, a shellfish biologist with decades of applied research experience, who agreed with MacKenzie early on that this project was worth doing, that it "makes sense" even if we can't readily find out whether and to what extent it works.

A major challenge is to find ways to evaluate and justify projects such as this one that may not ever be amenable to scientific testing. Nature is complex, various, and illusive. Experimentation outside the laboratory is difficult, often impossible. Our team's attempts to develop experimental means of evaluating spawner sanctuaries "in the wild," led by Fegley, continue, but there is persistent trouble convincing peer reviewers that they are scientific enough. Yet research of that kind is essential if science is to affect shellfish enhancement policy. New ways to communicate and interact, as suggested by Ravetz (1986), perhaps based on the co-management experience, may help us to become more discriminating in reaching the conclusion offered by biologists at the outset of our spawner sanctuary project: Just do it. It makes sense.

ACCOMPLISHMENTS

I have dwelt at length on the disappointments and failures of the project because of what they reveal about the social reality of very different people trying to work together. Our accomplishments should not be underestimated. They were many, and they were the outcome of the cooperation of these very different people, trying to cope with each other, the lack of knowledge, and themselves.

Our accomplishments included these:

1. two large spawner sanctuaries were created in 1986, and several small, experimental ones were created in subsequent years;
2. scientific research to evalute the success and rationale for spawner sanctuaries was begun in 1986 and received more support in 1987 and 1988;
3. a position in applied hard clam research was created by the Fisheries Technology and Aquaculture Extension Center in 1987.
4. Because of involvement in this project, MacKenzie established an ongoing study to control hard clam predators.
5. the Fisheries Development Commission created a Hard Clam Research Committee in 1987; headed by myself, it is a forum for continued cooperation among clammers, state officials, and scientists in identifying problems, exploring possible solutions, and planning for hard clam enhancement;
6. recognizing limitations of spawner sanctuaries, participants in the project have explored and become involved in alternatives, including small-scale, "intermediate technology" mariculture, ranging from hatchery operations to simple "growing-out" ventures.

I think we also,

7. showed ourselves and others that it is indeed possible, if not always pleasant or productive, for members of the industry, academic scientists, government scientists, and administrators to cooperate.

The last word belongs to Bill Jenks. Before he left the project, upset about the state's seeming neglect of their responsibilities and by what he saw as the over-objectivity and skepticism of the scientists, Bill Jenks agreed to evaluate the program (pers. comm. 10/26/86):

> "So, what have we done in the last two years? We have completed two "hard clam spawner sanctuaries" and have started a new trend towards biological enhancement! Many people are thinking CLAM. We changed the thinking of many people in State government through dogged determination. We attended many meetings to try to cut through the red tape and succeeded . . . We aided the shellfish industry and gave them new ideas and guidelines. The word "hard clam spawner sanctuary" is now a word being used daily along the entire N.J. coast. And who knows? It might work!"

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THE REPRODUCTIVE CYCLE OF THE ROCK SCALLOP *HINNITES GIGANTEUS* (GREY) IN HUMBOLDT BAY, CALIFORNIA

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ABSTRACT The annual reproductive cycle of the rock scallop *Hinnites giganteus* (Grey) from Humboldt Bay, Northern California, was examined. Rock scallops were collected at 3–6 week intervals between June 1984 and June 1985 and histological sections of the gonad were made. A poorly defined annual spawning cycle was observed. Scallops were in the active or ripe stages throughout most of the year. Induced spawning, attempted at 3–6 week intervals by injecting serotonin into the gonad, was successful in both sexes every month but November 1984 and January and February 1985.

KEY WORDS: gametogenesis, *Hinnites giganteus*, rock scallop, spawning cycle.

INTRODUCTION

Rock scallops *Hinnites giganteus* (Grey 1825) inhabit rocky substrata, both inter- and sub-tidally from Baja California to Northern Alaska (Yonge 1951). Wild stocks of rock scallops in Northern California have been significantly reduced by sport harvest, and as the popularity of SCUBA diving increases, fishing pressure will probably increase (Ronald Warner, California Fish and Game, Eureka, CA). This rising demand for scallops could be met with a seeding program to enhance wild stocks. California has a supplemental seeding program for the red abalone, *Haliotis rufescens* (Swainson 1822) and it is possible that similar programs could be developed for rock scallops. Rock scallops are also a potential mariculture species (Leighton and Phleger 1977).

For both restocking and mariculture purposes, it is essential to know the life cycle of rock scallops. Documentation of the reproductive cycle in a fishery is one logical step in determining when recruitment might occur. The periodic examination of gonadal tissue has proven to be a reliable method of determining seasonal gonadal changes in rock scallops (Lauren 1982). Also, laboratory stimulation of spawning has been used to measure ripeness, and is of particular interest to mariculturists as a precursor to hatchery production (Leighton and Phleger 1977, Cary et al. 1981).

Studies of the reproductive cycle of rock scallops have been conducted in Puget Sound, WA (Olson 1980, Lauren 1982, Bronson et al. 1984) and at San Diego, CA (Leighton and Phleger 1977). A comparison of these studies shows a variety of reproductive patterns. Rock scallops of Matia and Suchia Islands, Upper Pugent Sound, WA began active gametogenic development in January, became ripe in May and spawned in June (Lauren 1982). Spontaneous spawning was observed from September to December in Hood Canal, Puget Sound, WA (Bronson et al. 1984). A bimodal spawning season was also observed in Puget Sound near Brinnon, WA, first in May and again in September (Olson 1980). Histological evidence indicated that spawning occurred in the Spring and Fall for rock scallops of San Diego, CA (F. Jacobson, University of San Diego, San Diego, CA). Induced spawning, by a variety of methods was done successfully throughout most of the year in San Diego, CA (Leighton and Phleger 1977, Leighton 1979, 1981).

The present study was undertaken to determine the annual reproductive cycle of rock scallops in Humboldt Bay, CA. Histological and induced spawning results were compared to similar studies done in San Diego, CA and in Puget Sound, WA. Environmental variables at these locations were compared to those in Humboldt Bay to determine if there was any correlation between these variables and corresponding reproductive cycles.

MATERIALS AND METHODS

A total of 170 scallops was collected by SCUBA divers from June through September 1984 off the Samoa Bridge pilings in Humboldt Bay, CA (40°49′N, 124°10′W) (Figure 1). Scallop heights range from 9.5 to 16.0 cm and the length ranged 8.0 to 14.0 cm. Scallop ages ranged from 3–7 years. The scallops were transported 1 km. South to the Washington Street dock (Figure 1) and placed in lantern nets. Nets were suspended from the dock such that the lowest compartment was 1 m above the bottom and the highest compartment was 3 m below MLLW. Surface temperatures were taken at 3–6 week intervals and ranged from 9.3—16.0°C (Table 1).

The gonads were removed from 115 scallops at 3–6 week intervals from June 1984 to June 1985. Twelve samples, ranging in size from 8 to 10 individuals, were examined. Histological procedures followed those outlined by Humanson (1962). Gonadal tissue, 4 mm thick, was fixed in alcohol-formalin-acetic acid (AFA) for 24 hours,

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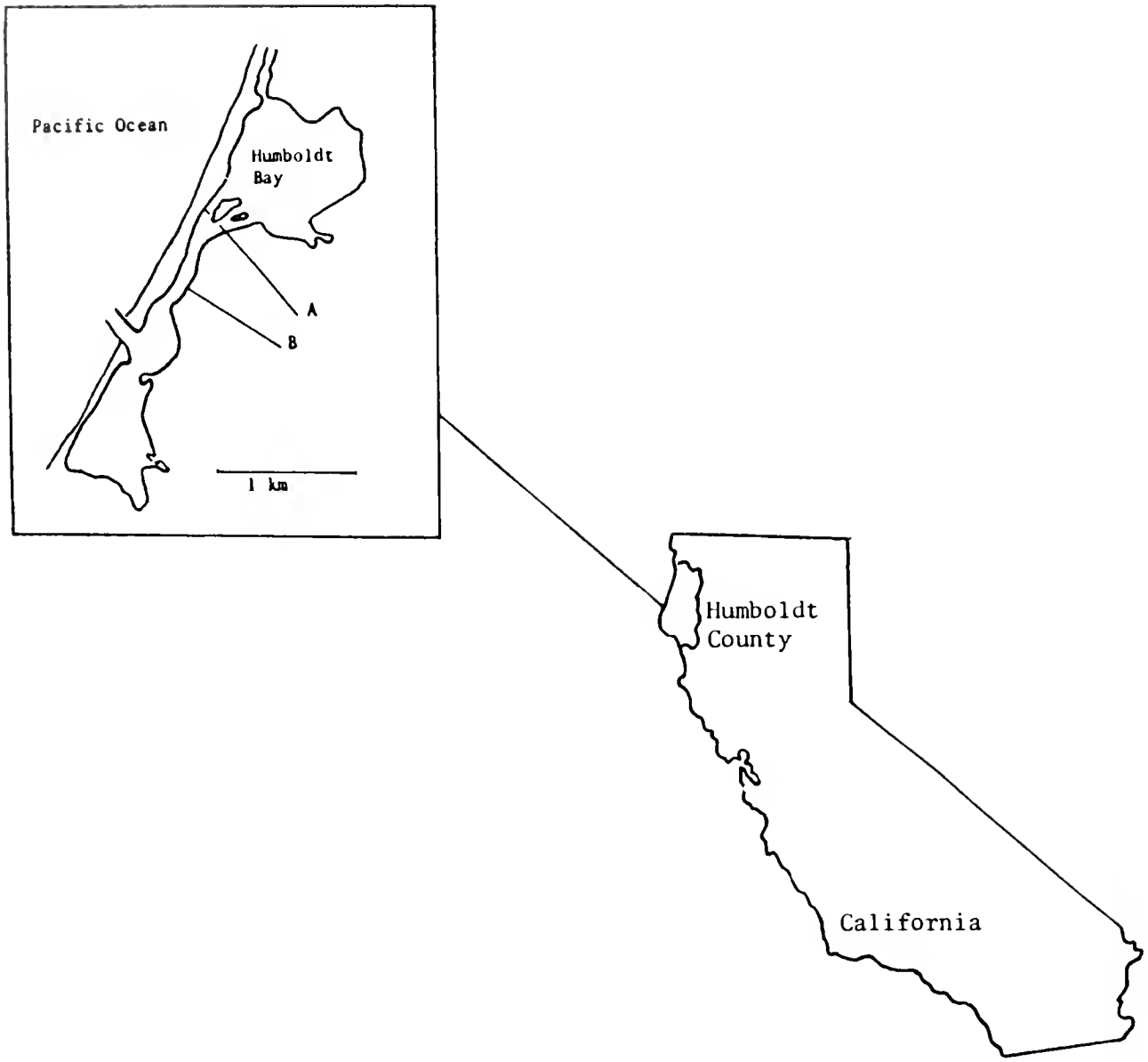

Figure 1. Locations of collection and sampling sites in Humboldt Bay, California. (A) Samoa bridge, located at the northwest end of Indian Island: collection site. (B) Washington street dock: holding site.

dehydrated using serial dilutions of absolute and isopropyl alcohol, and infiltrated with and embedded in paraplast. Embedded tissue was sectioned at 6 um. Sections were placed on slides covered with a thin layer of Haut's adhesive, and a drop of formalin was put on each section. The slides were placed on a warming table until the formalin evaporated. Paraplast was removed by dipping the slides in xylene. Tissue was rehydrated using a series of dilute alcohol solutions and the sections were stained with Erlickman's hemotoxylin and eosin.

Definitions of Gametogenic Phases

The reproductive cycle was divided into five stages similar to those used for *M. arenaria* by Ropes and Stickney (1965):

1. active,
2. ripe,
3. partially spawned,
4. spent, and
5. indifferent.

Photomicrographs of various stages were taken with a standard Olympus microscope and camera at magnifications of 100 and 200×.

Indifferent (Figure 2a)

The indifferent gonad consisted of basophilic vesicular connective tissue that contained follicles that were either empty or contained pycnotic cells. Sex cells, even in their earliest stages of development, were absent. Sex determination was not possible.

TABLE 1.

Number of Scallops sampled for histological investigation and Humboldt Bay water surface temperature from June 1984 to June 1985.

Date	Number of Scallops Sampled	Bay Water Surface Temperature
6/84	9	15.8
7/84	10	15.9
8/84	8	15.8
9/84	10	13.3
10/84	10	13.0
11/84	10	11.0
1/85	10	9.3
2/85	10	11.0
3/85	10	10.0
4/85	10	13.4
5/85	9	12.8
6/85	9	16.0

The Ovary

Active (Figure 2b). The active phase was characterized by the presence of ova in all stages of development, from immature ova on the follicle wall to stalked oocytes and fully developed ova free in the lumen. As the number of mature ova increased, the amount of connective tissue decreased. The active scallop ovary exhibited the "solitary" type of oocyte formation described by Raven (1958), where each oocyte develops from a single cell of the germinal epithelium.

Ripe (Figure 2c). The ripe ovary exhibited distended follicles filled with detached mature ova 80 um in diameter. Only a few stalked oocytes remain. Little or no connective tissue was present.

Partially Spawned (Figure 2d). Some follicles were empty while others contained eggs. Redeveloping oogonia lined the follicular walls of the empty or nearly empty follicles. More connective tissue was present than in the ripe phase.

Spent (Figure 2e). The follicles were empty except for redeveloping oogonia lining the walls. The connective tissue between follicles was more prevalent than in the partially spawned stage.

The Testis

Active (Figure 3a). Stem cells, spermatagonia, spermatocytes, spermatids and a few spermatozoa were present from the follicle wall to the center of the lumen. The amount of connective tissue present varied between follicles, decreasing at more advanced stages.

Ripe (Figure 3b). The follicles were distended and filled with mature spermatozoa. Little or no connective tissue was present. Early stages of spermatogenesis were absent.

Partially Spawned (Figure 3c). Follicles in this phase were partially empty, with gaps between rows of spermatozoa. The amount of connective tissue between follicles increased.

Spent (Figure 3d). The follicles were collapsed or had decreased in size. A few follicles contained a small amount of unspent spermatozoa.

Induced Spawning

A number of methods have been used to induce spawning in bivalves. These techniques include ultra-violet treated water (Uki and Kikuchi 1974), increasing water temperature 5°C (Cary et al. 1981) and adding sperm suspension to tanks containing both females and males (Leighton and Phleger 1977).

Serotonin (5-hydrooxytryptamine, creatine sulfate complex) has been used as an effective chemical method to stimulate spawning in bivalves that have been historically difficult to spawn (Matsutani and Nomura 1982). For example, spawning has been induced in the ocean quahog, *Artica islandica* (Linne) by injecting serotonin into the gonad (Gibbons et al. 1983).

Serotonin occurs naturally in the cerebropleural, pedal and visceral ganglia of *A. islandica* (Welsh and Moorhead 1960). This chemical is a neurotransmitter, but its physiological role as an inducer of spawning in bivalves is not thoroughly understood (Gibbons et al. 1983). The advantage of this technique is that spawning response is rapid and synchronous when applied to ripe individuals.

Induced spawning was attempted every 3–6 weeks by injecting the gonads of two males and two females with 0.4 ml serotonin solution, made by dissolving 7.7 mg. of serotonin in 10 ml of heated 0.8 um filtered sea water (Gibbons et al. 1983). When both sexes spawned, the gametes of each were mixed to determine whether a fertilization membrane formed. If a membrane formed, the gametes were considered viable.

RESULTS

Reproductive Cycle

The annual reproductive cycle of rock scallops from Humboldt Bay is summarized in Figure 4. Most scallops were either in an active or ripe phase throughout the year. Ripe individuals were found every month except in March and June 1985. The ripe phase predominated (over 50% of the animals) in August, September, and November 1984. Rock scallops in the active phase were seen every month and predominated in June 1984 and April, May and June 1985. Partially spawned scallops were observed in August, September and October 1984 and January, February, March, May and June 1985. Spent scallops were noted in October 1984 and January, March and June 1985. These results indicate a poorly defined annual spawning cycle.

Induced spawning

Induced spawning occurred each time it was attempted, but during some months not all four animals responded

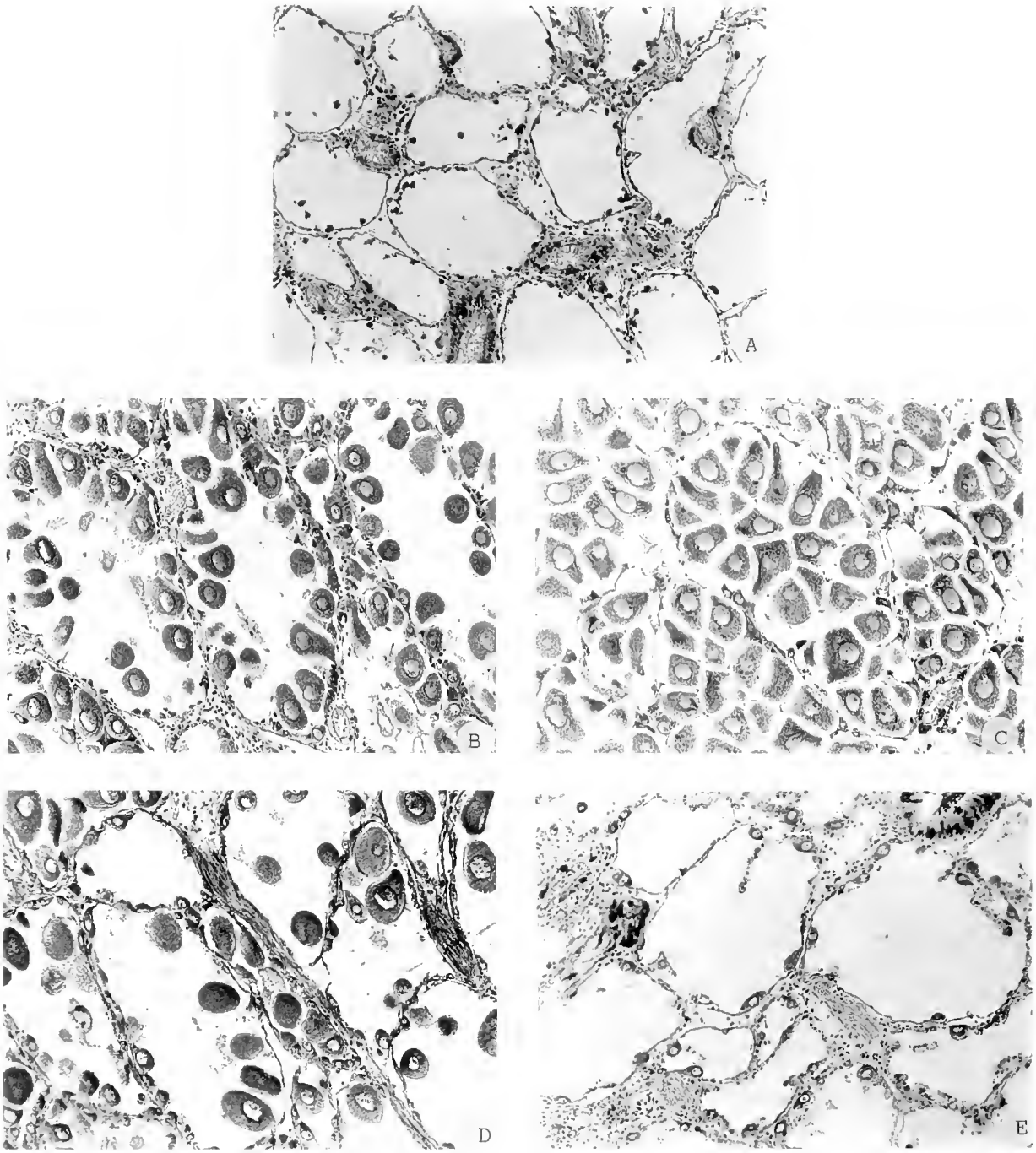

Figure 2. Photomicrographs of gonadal stages of female and indifferent *Hinnites giganteus* at 100× magnification. a) Indifferent unsexed, b) Active female, c) Ripe female, d) Partially spawned female, e) Spent female.

(Figure 5). In October and November 1984 and January 1985 only one female spawned. In February 1985, two males spawned, while in October 1984 only one female and one male spawned. In all other attempts all four animals spawned. One half to 2 hr. after injecting serotonin, valve clapping began and spawning occurred 15 min. later. Every time females and males both spawned, the mixed gametes produced a fertilization membrane, indicating viable gametes.

DISCUSSION

Reproductive Cycle

The results of gonadal examination showed no clearly defined seasonal reproductive cycle for rock scallops in Humboldt Bay, CA. Spawning seems to occur throughout the year in a poorly defined pattern similar to that described by Edwards (1984) and Skidmore and Chew (1985) for the mussel *M. californianus* from Trinidad, CA and Puget

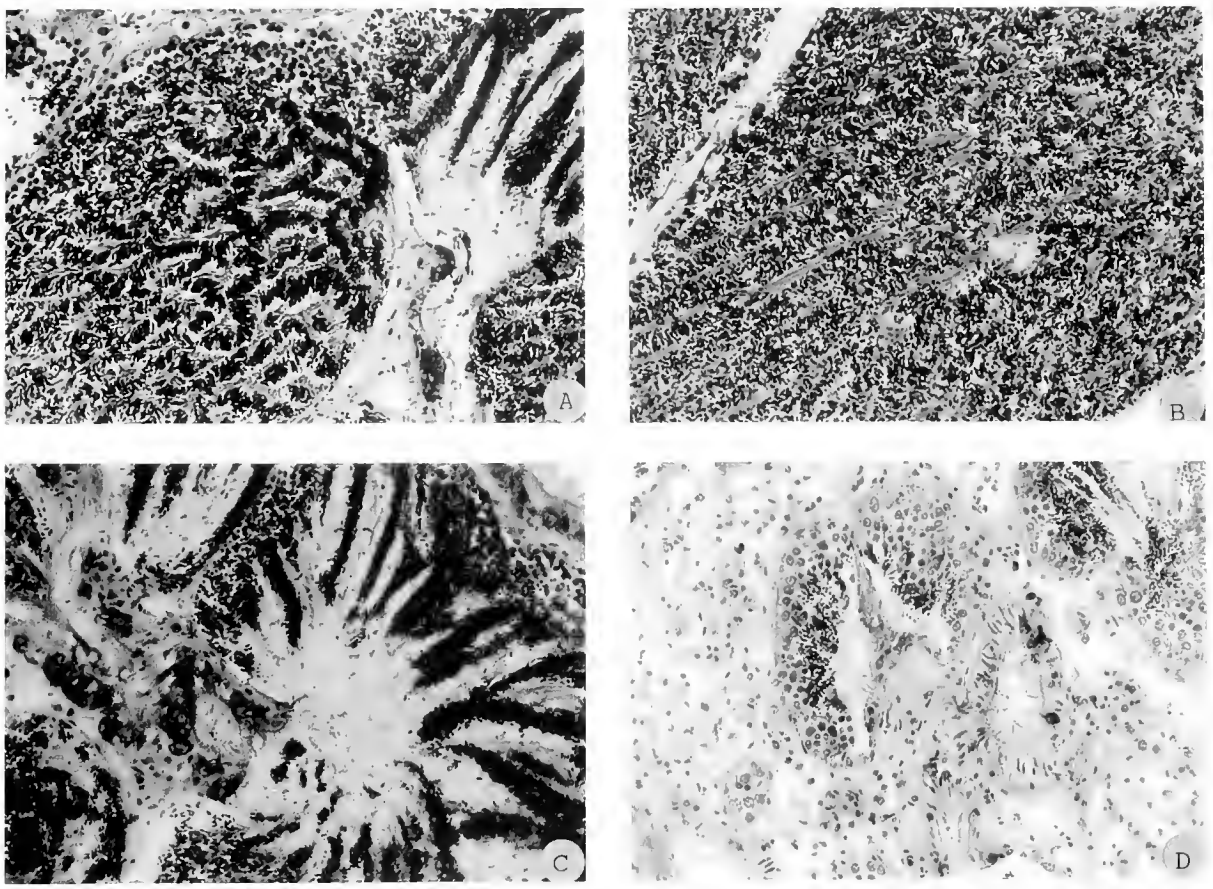

Figure 3. Photomicrographs of gonadal stages of male and Hermaphrodite *Hinnites giganteus* at 200× magnification. a) Active male, b) Ripe male, c) Partially spawned male, d) Spent male.

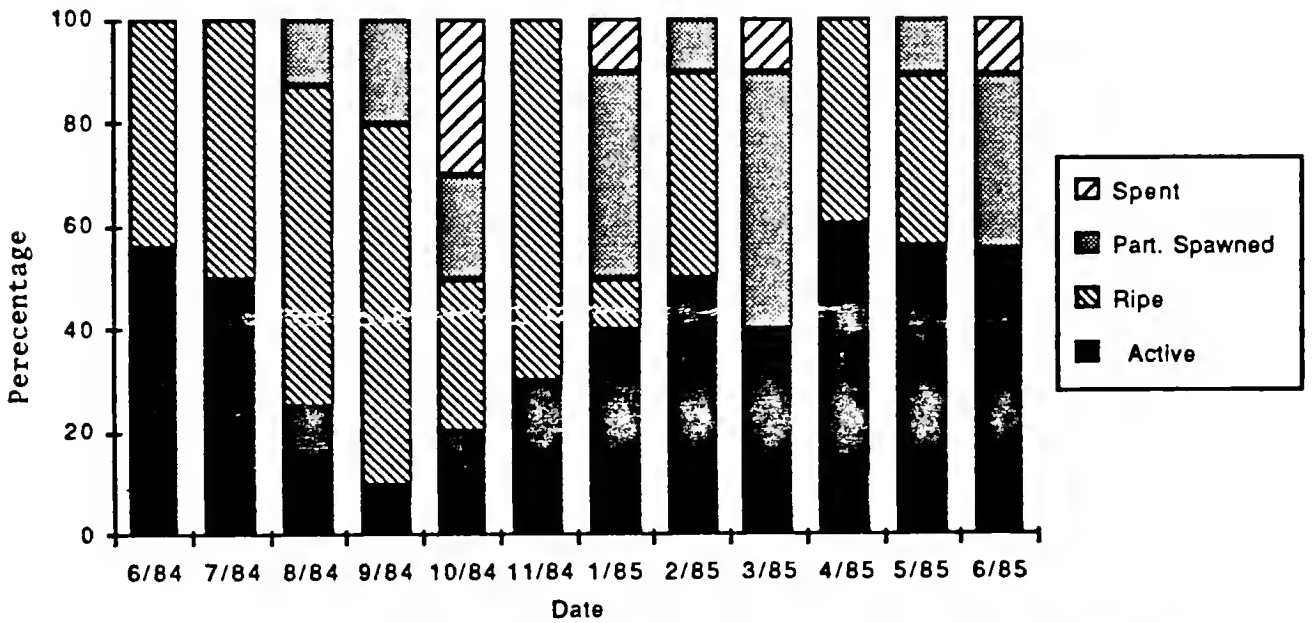

Figure 4. Gametogenic phases of rock scallops (*Hinnites giganteus*). The height of each designated area represents the percentage frequency of scallops in each phase, June 1984 to June 1985.

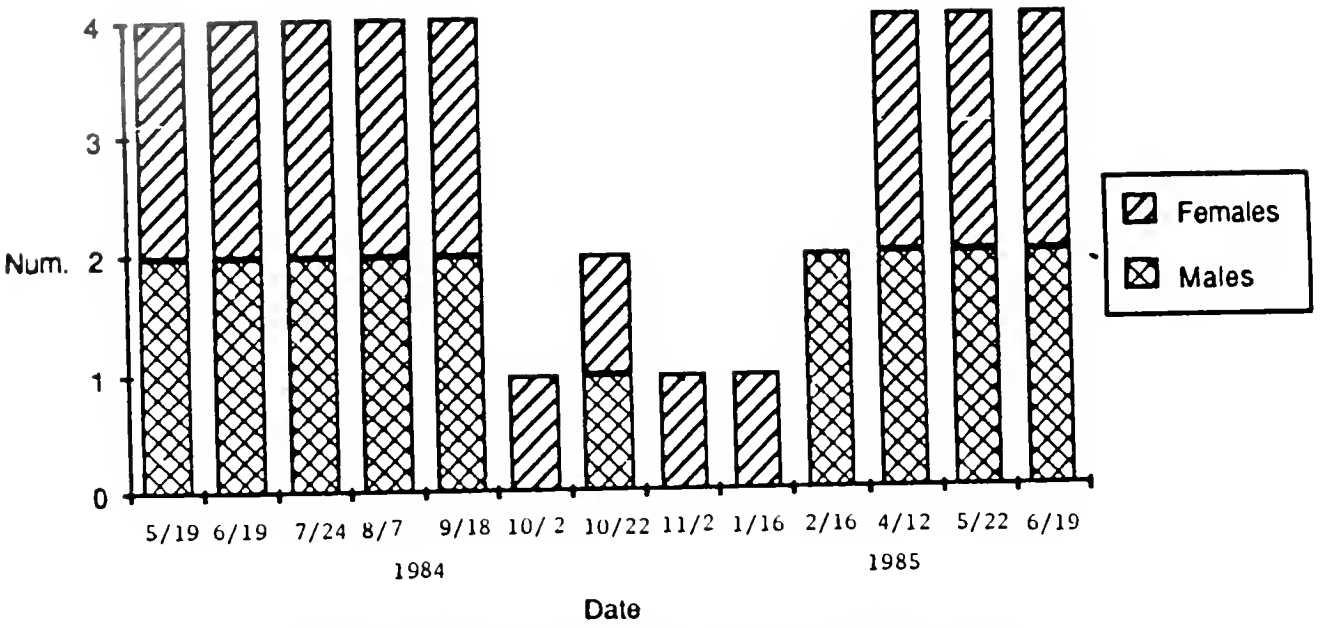

Figure 5. Induced spawning success of four injected adults (*Hinnites giganteus*).

Sound, WA. Spawning in these mussels, which have a poorly defined reproductive cycle, was characterized by a slight reduction in the density of spermatazoa in a limited area of the follicle.

In rock scallops from Humboldt Bay, partially spawned and spent gonads were observed in most months sampled. Active gametogenesis was observed throughout the study period, and ripe individuals were seen in all months sampled except March and June 1985. Because of small sample size, results for male and female gonadal development were combined in Figure 4. Separate descriptions of male and female gonadal conditions reveal a tendency for both sexes to constantly maintain a high degree of spawning ability. All females in the spent and partially spawned phase had developing oogonia on the follicular walls, indicating that redevelopment was occurring during spawning (Figures 2d and 2e). Spent males usually retained some spermatozoa in a small percentage of follicles (Figure 3d).

Settling of rock scallops in Humboldt Bay occurs from June through November (William Osborne, Humboldt State University, Arcata, CA) Assuming at least one month of larval life (Leighton and Phleger 1977), spawning must have occurred from May to October, 1984. Partially spawned scallops were found in most months when spawning was estimated using settlement data. In the other months, June and July, ripe males were found and induced spawning was successful. This suggests that spawning may occur in the bay to a greater degree than indicated by partially spawned scallops. It is possible that rock scallops may spawn throughout the year in Humboldt Bay, but collectors were not out in Winter, so settlement during this period is not known.

The amount of time it takes for molluscs to recover from spawning varies with species, geographic location and environmental conditions. Rapid recovery following spawning was noted in mussels (*M. californianus*) from Chatman Island, B.C., Canada (Kelley et al. 1982). They noted that the active phase of the mussels lasted approximately 10 days, and the animals were capable of spawning during all of the observed histological stages. No spent phase was observed. The gonadal recovery period for the red abalone *Haliotis rufescens* ranged from 75–90 days for laboratory and 120 days for field specimens (Ault 1985). The red abalone has an annual reproductive cycle, and no partially spawned phase. There are no data on rock scallop gonadal recovery duration, but the presence of developing oogonia on the follicular walls in both the partially spawned and spent phases suggest that recovery may be relatively rapid.

A poorly defined reproductive cycle may be an adaptation that reduces the impact of larval mortalities due to unpredictable adverse conditions by insuring the survival of at least some larvae in cases where populations are periodically exposed to unfavorable conditions. (Skidmore and Chew 1985). This reproductive behavior may be a response to local and annual conditions that enhance recruitment (Kelly et al. 1982).

Reproductive and Environmental Factors

Several environmental factors may influence the timing of reproduction in bivalve molluscs. The most commonly cited are water temperature, food availability and tidal influence (Sastry 1966, Machell and DeMartini 1971).

Water Temperature

Previous authors have attempted to explain reproductive timing in bivalves primarily in terms of water temperature and its variation with latitude (Loosanoff 1937, Ropes and Stickney 1965, Newell et al. 1982). Bivalves in higher Northern latitudes tend to spawn in a single annual event of short duration while those in lower Northern latitudes have more extended and frequent spawning patterns (Sastry 1966, 1970). A comparison of rock scallop spawning behavior along the west coast of the United States does not show this correlation between latitude and reproductive cycle.

Food Availability

Time of spawning may also be related to food availability. Most bivalves tend to spawn during periods when food is available for developing progeny and for replenishing the energy adults spend in spawning (Bayne 1976). Chlorophyll concentrations (which may be related to food availability) peak in Humboldt Bay during June (Pequegnat and Butler 1982). Spawning during these months was not indicated by histological data suggesting there is no correlation between food availability and spawning.

Tidal Influence

Tidal influence may be a causative factor in reproductive timing. Only during the lowest tides of the year is a small percentage of scallops exposed to air; in most cases scallops are found sub-tidally. The scallop populations are located in or near dredged or tidally scoured channels. Tidal currents are swift in these areas, having velocities up to 50 cm/s during peak flow (John Pequegnaut, Humboldt State University, Arcata, CA). Poorly defined spawning cycles may be an adaptive response by bivalve populations to maximize their reproductive potential in areas where frequent and extreme tidal fluctuations have a deleterious affect on larvae (Kelly et al. 1982). As planktonic larvae are carried away from the vicinity of their beds at low tide, their opportunities for locating and settling on a suitable substratum are reduced (Bayne 1976).

Induced Spawning

The injection of serotonin into the gonad was a reliable method for inducing spawning of rock scallops from Humboldt Bay, CA (Figure 5). The seasonally independent ability of scallops to spawn correlates with my histological results and shows that scallops are ripe most of the year.

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Journal of Shellfish Research, Vol. 7, No. 3, 349–357, 1988.

EFFECT OF TEMPERATURE ON LARVAL DEVELOPMENT OF THE SPINY SCALLOP, *CHLAMYS HASTATA* SOWERBY, WITH A NOTE ON METAMORPHOSIS

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ABSTRACT Larval growth and survival of the spiny scallop, *Chlamys hastata* Sowerby, was examined at 12, 16, 19, and 24°C. Larvae reared at 12°C developed slower (42 days vs. 34 days), reached a larger maximum size (238.8 ± 0.93 μm vs. 231.0 ± 0.84 μm), and had better survival (42% vs. 33%) than larvae reared at 16°C. At 19 and 24°C larvae did not survive to metamorphosis. An inverse relationship between valve length and developmental time was observed. Throughout development, a linear correlation of 1.1:1 was observed between valve length and valve height ($r^2 = 0.95$). *C. hastata* larvae metamorphosed if a fouled substrate or a flow of water was present. Larvae did not settle gregariously, but tended to settle along edges and corners of objects than on planar surfaces. Larvae did not always metamorphose after a specific time period and could survive for up to 120 days (12°C). The age of larvae influenced the rate of settlement and metamorphosis with a reduced response observed as maximum age was reached.

KEY WORDS: *Chlamys hastata*, Pectinidae, larval development, temperature, metamorphosis

INTRODUCTION

Success and rate of larval development of many marine species that have a planktonic larval stage is affected by physical or endogenous parameters. Among physical parameters, temperature is probably the most frequently investigated because it can be easily manipulated and has a significant effect on growth and survival (e.g., Davis and Calabrese 1964, Lough and Gonor 1973, Tettelbach 1979, Falmagne 1984). These and other studies have shown that growth to setting size, and therefore completion of the larval period, generally is more rapid as temperature increases to some optimum level, and then declines with further temperature increases (Bayne 1983).

Upon completion of larval development, bivalve larvae undergo metamorphosis into the juvenile stage and this can be affected by a variety of stimuli, such as surface textures and contours, chemical 'inducers', and bacterial films (Meadows and Campbell 1972, Crisp 1974, Burke 1983). In the natural environment, therefore, it is believed that larvae settle in a nonrandom pattern. Length of the larval period in some marine invertebrates is known to be prolonged if a site for settlement is not located or particular stimuli are not encountered (Bayne 1965, Crisp 1974, Sastry 1979).

Spiny scallops, *Chlamys hastata* Sowerby, are widely distributed in the northeast Pacific from 33–60°N in depths of 2–150 m (Bernard 1983). In British Columbia they occur in small beds that are scattered along the coast, usually on firm rock or gravel bottoms in areas of strong currents. Spiny scallops rarely attain a shell height larger than 80 mm.

There is little biological information on spiny scallops and nothing on the life history of this species. The present study was part of a larger work describing morphological development of *C. hastata* larvae (Cooke 1986) and presents data on the effect of temperature on larval development of spiny scallops along with observations on metamorphosis.

MATERIALS AND METHODS

Spawning and Larval Rearing

Adult *C. hastata* were collected by SCUBA near Wizard Rock in Barkley Sound, British Columbia from a depth of 20–30 m (Figure 1). Animals were kept for two to five weeks in a darkened, 20 L tank that had a continuous flow of seawater (14–16°C) at the Bamfield Marine Station. Three times daily, the water was turned off for one hour and several litres of supplemental cultured phytoplankton ($2–3 \times 10^6$ cells/ml) were added.

Spawning of conditioned animals was induced from June through September, 1982. Epifauna were removed from the shells, and the sexes segregated in polyethylene buckets prior to spawning. A slow, continuous flow of UV-irradiated seawater was dripped into the buckets, and the water was warmed from 12° to 16–18°C over a period of one to two hours. Males generally spawned after 20 to 60 minutes, but females took up to three hours to spawn. After one adult spawned, others in the bucket usually spawned.

Gametes were collected and immediately washed with 0.8 μm. glass-filtered seawater. The oocyte suspension was passed through a 253 μm nitex screen to remove debris, collected on a 20 μm screen and rinsed carefully. The sperm suspension was passed through a 100 μm screen, added to the oocytes and left for 6–10 min. Fertilized oocytes were collected on a 20 μm screen, rinsed to remove excess sperm and transferred to 4 L beakers containing 0.45 μm membrane-filtered seawater (12°C). Water

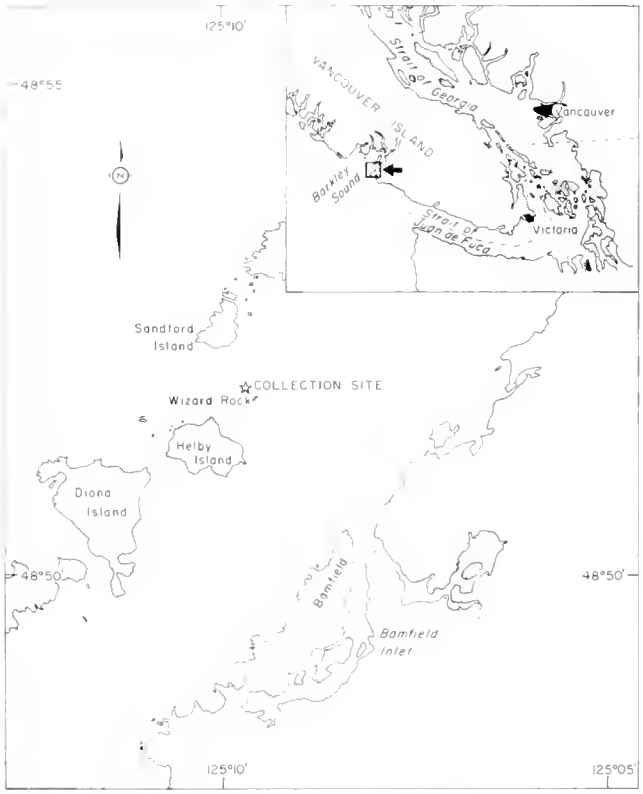


Figure 1. Collection site of adult *Chlamys hastata* in Barkley Sound, British Columbia.

was decanted and replenished twice during embryonic development.

Larvae were reared using methods adapted from Loosanoff and Davis (1963). Approximately 50 hours after fertilization, D-stage veliger larvae were transferred to 2 L beakers containing 0.45 μm filtered seawater to which 50 mg/L streptomycin sulphate and 2 mg/L chloramphenocol was added. Larvae were fed a mixture of unicellular phytoplankton daily in concentrations of $10-40 \times 10^4$ cells/ml. Phytoplankton species used in this study included *Nannochloris atomus, Pavlova lutheri, Isochrysis galbana, Thalassiosira pseudonana* and *Dunaliella tertiolecta*. Seawater was changed and larvae were transferred to clean beakers every two or three days.

Temperature Effects on Larval Development

Larval growth and survival was determined at four temperatures, 12, 16, 19, and 24°C. For 1.5 L beakers, each containing 3500–4500 D-stage larvae in 750 ml of 0.45 μm filtered seawater (salinity 31–33‰), were held at each temperature. One beaker held at each temperature was sampled to estimate survival during development. Each beaker was agitated during sampling using a perforated plunger to ensure even distribution of larvae. Twenty, 5-ml samples were collected every 6 days and an average value for larval density was calculated. Estimates of survival were recorded on subsequent days as a percentage of the initial stocking density (5–6 larvae/ml). Valve length and height of 70 larvae from the remaining three beakers at each temperature were measured every 6 days. All measurements were made to the nearest 4.5 μm with a compound microscope fitted with an ocular micrometer. The experiment was terminated when larvae were determined to be capable of metamorphosing into juveniles.

Growth data were analyzed using Student's T-test and Duncan's multiple range test. Correlation between length and height measurements was examined using linear regression analysis.

Metamorphosis

Larvae used for metamorphosis experiments were reared at 16°C. Criteria used to determine larval maturity included size, morphology, and behavior. Mature larvae were at least 34 days old and were 230 μm in length. Presence of eyespots, a well-developed foot, and developing gill bars, as well as such behavior as foot extension while swimming or crawling were also used to identify mature larvae.

The percentage of larvae that successfully metamorphosed was determined by counting the number of postlarvae firmly attached to a surface 24 hours after initiation of a given trial. This estimate was confirmed by counting the number of metamorphosed individuals 1 day later. Postlarvae were identified by morphological features that could be observed using a dissecting microscope: lack of velum, presence of gill bars with elongated primary filaments, and orientation of the foot in a ventral or anterior position rather than a posterior position as found in the larval stage. Unless otherwise stated, each replicate consisted of 50 larvae placed in a 100 × 50 mm Pyrex dish containing 100 ml of 0.45 μm filtered seawater (16°C) and the test substance. Controls of each trial consisted of 50 larvae in a dish containing 0.45 μm filtered seawater (16°C).

Various cultch-type materials and chemicals were tested individually for their effect in stimulating larvae to metamorphose. Pieces of scrubbed and autoclaved scallop shell and frayed polypropylene line were added to test dishes. An extract of adult scallops was prepared by grinding and centrifuging whole tissue in a small quantity of filtered seawater. Small aliquots (5–10 ml) of the resulting supernatant were added to experimental dishes. Different concentrations of GABA (Gamma-aminobutyric acid) (Sigma Chemical Co.) (10^{-3}, 10^{-4}, 10^{-5} M) and L-Dopamine (Sigma Chemical Co.) (10^{-3}, 10^{-4}, 10^{-5}, 10^{-6} M) were also added to test dishes. Pieces of glass slides and paraffin plastic (Parafilm) which had been placed in running seawater for approximately 10 days prior to the experiment to allow colonization of micro-organisms were used as fouled surfaces. Control dishes contained glass slides or paraffin plastic that had been cleaned. Rates of metamorphosis in experimental dishes with and without fouled surfaces were compared using the Wilcoxon paired-sample test.

To determine the effect of flowing seawater on the rate of metamorphosis, groups of 50 larvae were placed in plastic containers with 102 μm nitex mesh bottoms through which passed a slow (~200 ml/min) continuous flow of 1 μm glass-filtered seawater. Larvae placed in nitex containers set in Pyrex dishes filled with filtered seawater that was changed daily served as a control. The temperature for all containers was 12°C. Data were tested for significant differences using the Wilcoxon paired sample tests.

The influence of a combination of fouled surface and water flow on metamorphosis was tested by two-factor analysis. Groups of 50 larvae were placed in nitex containers and provided with a flow of seawater, a fouled surface (glass slide with a flora of micro-organisms), or both. Larvae placed in nitex containers set in Pyrex dishes filled with filtered seawater served as controls. Differences in the number of larvae that metamorphosed were tested using a two-way analysis of variance (unequal n).

The orientation and position of postlarvae on a piece of glass slide was examined to determine whether settlement was gregarious. The area of the slide was divided into quadrats and the frequency of distribution of postlarvae was tested for agreement with a random (Poisson) distribution.

The time when *C. hastata* larvae were first able to metamorphose was determined by placing larvae of a known age with a stimulus or stimuli that were shown to induce metamorphosis in previous experiments. Larvae reared at 12°C and 16°C were used and ranged in age from 22–45 days. Metamorphosis was calculated as described above. Larvae of different ages, between the time when they were mature and maximum age, were also tested to determine whether age affected the larva's ability to metamorphose.

RESULTS

Temperature Effects on Larval Development

Larval survival declined sharply during the first two weeks at all temperatures, but less so at 12°C (Figure 2). Larvae reared at 24°C were all dead by day 15. Larvae raised at 19°C showed a continuous steep decline in numbers throughout the experiment, with 40% surivival at day 15 and complete mortality by day 40. Larval survival at 16°C declined sharply until day 15, at which time there was 44% survival. Mortality then tapered off and survival was 33% on day 40. At 12°C larval survival showed the least decline with 61% at day 15 and 42% on day 40.

In the experiment to determine the effect of temperature on larval growth, greater variance was found between treatments than between replicates and, therefore, data were pooled for analysis. Initial valve length at day 3, the start of all experiments, was 112.0 ± 0.85 μm (Figure 3). Growth at 24°C was the slowest of any treatment, and by day 9, valve lengths of larvae held at the different temperatures were significantly different ($p < 0.05$, Table 1).

Initial growth rate of larvae reared at 19°C was similar to that of larvae raised at 12° and 16°C, but after day 9 the instantaneous growth rate of larvae reared at 19°C declined steadily over the 24 day period (Figure 4). During this time, larvae grew an average of 2.5 μm/day and reached a mean shell length of 182 μm by day 27. Work with larvae at this temperature was terminated after day 27 because of low numbers.

Until day 31, larvae raised at 16°C had a faster growth rate than those raised at 12°C (Figure 4). Eventually, larvae raised at 12°C reached a significantly larger mean length than larvae raised at 16°C (Students T-test, $p < 0.001$, Figure 3). Instantaneous growth rate of larvae raised at 16°C was 5.8 μm/day between days 9 and 21, and 1.95 μm/day between days 21 and 31. At 12°C, the instantaneous growth rate was 4.8 μm/day between days 9 and 27, and 1.58 μm/day between days 27 and 39. Little growth occurred after this time at either temperature.

Similar results were obtained when shell height was used as a measure of growth (Figure 5). Initial valve height was 85.9 μm. At day 44, mean shell height was 215.7 μm at 12°C and 209.9 μm at 16°C. The linear relationship between valve length and height ($y = .96x + 77$) was highly significant ($r^2 = 0.95$).

Metamorphosis

Larvae reached a maximum size of 230–240 μm in 31 days at 16°C and 39 days at 12°C. However, no evidence of

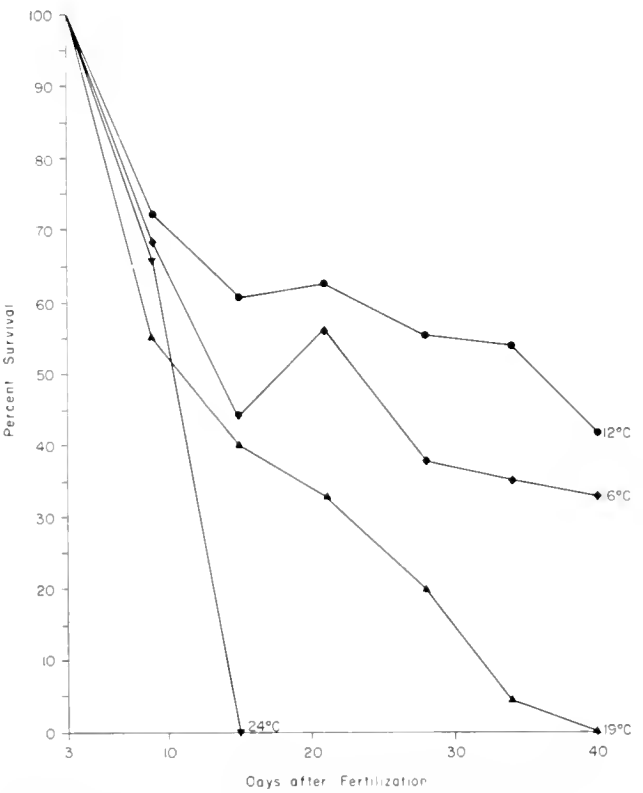


Figure 2. Percent survival of *Chlamys hastata* larvae reared at different temperatures.

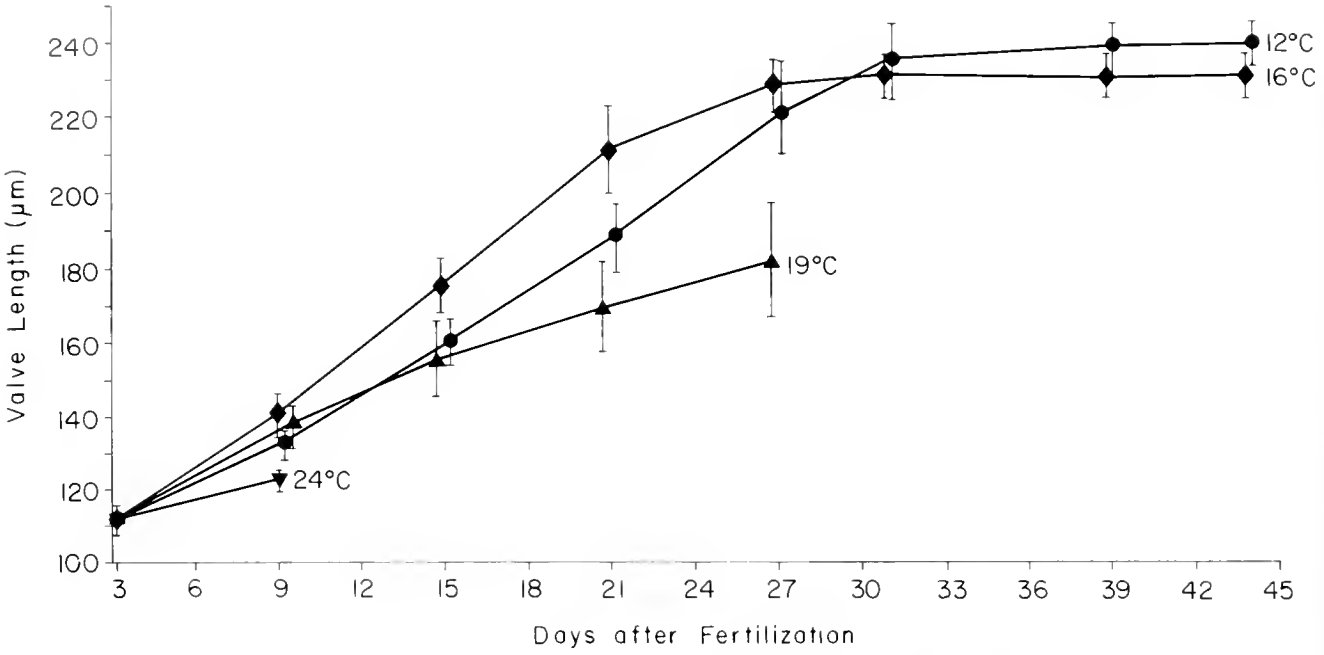


Figure 3. Valve lengths of *Chlamys hastata* larvae reared at different temperatures.

metamorphosis was observed until at least three days after maximum mean valve length was attained. Larvae were able to metamorphose after 34 days at 16°C or 42 days at 12°C. Larvae were held as long as 103 days at 16°C and 120 days at 12°C without metamorphosing. All age groups of larvae tested for their ability to metamorphose had some larvae metamorphose, except those within 10 days of maximum age (Table 2, Figure 6).

No larvae metamorphosed when placed in containers with pieces of adult shell, adult extract, or strands of polypropylene line (Table 3). Addition of GABA and L-Dopamine were also not effective in inducing *C. hastata* larvae to metamorphose. When higher concentrations of the chemicals were tested, they were found to be toxic.

Settlement and metamorphosis were observed only when fouled surfaces were present in containers. Results of the Wilcoxon paired sample test showed metamorphosis on fouled surfaces was highly significant when compared to settlement on clean surfaces (Table 4; $p < 0.0001$). A flow of seawater, simulating a current, also significantly enhanced the success of metamorphosis (Table 4; $p < 0.001$). A combination of a fouled surface and water flow resulted in the highest rate of metamorphosis ($p < 0.01$).

Larvae settled on surfaces in a non-random pattern with more larvae along edges and in corners than on planar surfaces. In nitex cups, larvae tended to settle in corners rather than on the screen or walls of the cup. In one experiment, less than 2% of larvae settled and metamorphosed on surfaces other than the edge of the slide, indicating a non-random settling pattern (Figure 7a). The area along the edge of the slide was divided into quadrats and the resulting frequency distribution was found to be random (Figure 7b; $p < 0.05$).

TABLE 1.

Results of Duncan's Multiple Range Test for valve lengths of 9-day old *Chlamys hastata* larvae reared at four temperatures. Values with different Duncan groupings are significantly different ($p < 0.05$).

Duncan Grouping	Temperature (°C)	Mean Valve Length (um)	Sample Size (n)
A	16	141.6	165
B	19	137.9	210
C	12	133.2	150
D	24	123.2	37

DISCUSSION

Temperature Effects on Larval Development

Initial high levels of mortality observed among larvae reared at all temperatures may have been a result of overcrowding and independent of temperature. Although initial densities of 5–6 larvae/ml have been described as satisfactory for some bivalve larvae (Jespersen and Olsen 1982, Disalvo et al. 1984), density dependent mortalities have been described by other workers (Loosanoff and Davis 1963, Gruffydd and Beaumont 1972). Work with *Patinopecten yessoensis* larvae indicated that the highest survival was attained when initial density was 2 larvae/ml (B. MacDonald, pers. comm.). It is possible that survival of *C. hastata* larvae would have been higher if initial densities had been ≤2 larvae/ml. However, a trend of decreased survival with increasing temperature was observed for *C. hastata* larvae with those reared at 12°C having the highest

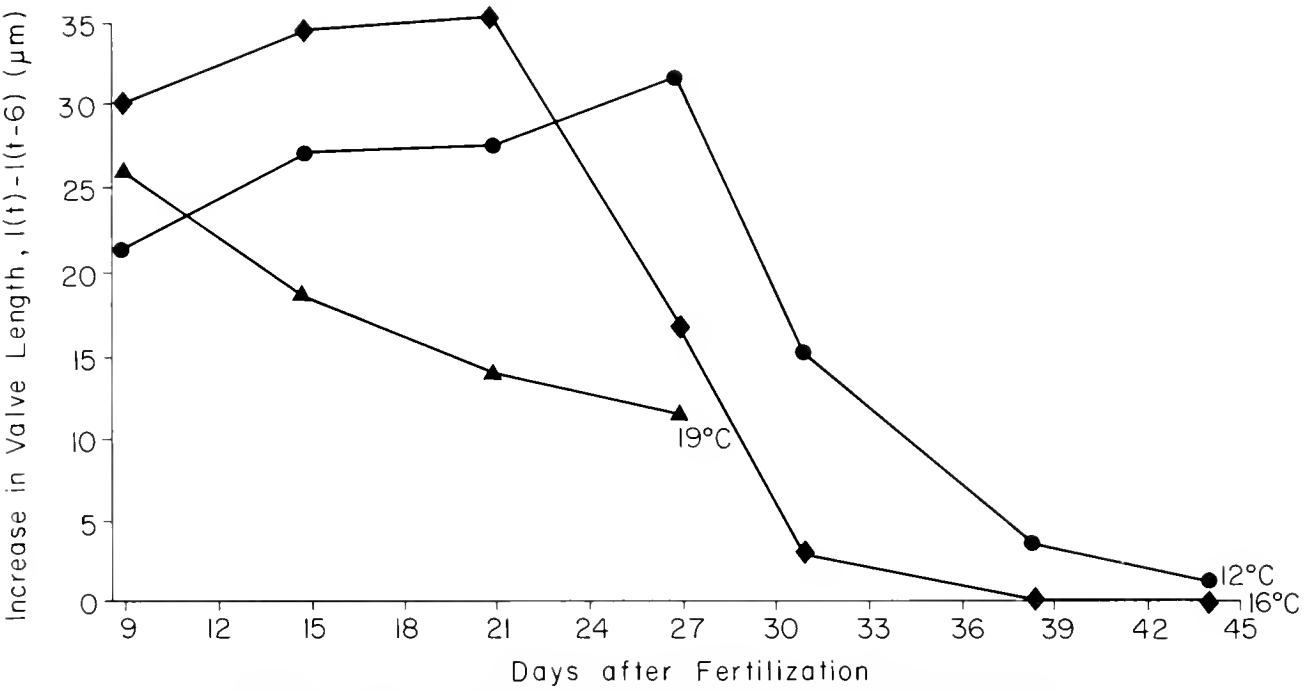


Figure 4. Instantaneous growth rate of *Chlamys hastata* larvae reared at different temperatures.

survival. Generally, larvae reared at temperatures close to their tolerance limits suffer higher mortality (Loosanoff et al. 1951, Ansell 1961).

Bivalve larval growth generally increases with temperature, up to some optimum level (Bayne 1983). However, a further increase in temperature causes growth to decline. This appears to be true for *C. hastata* where larval growth was faster at 16°C (5.8 μm/day) than at 12°C (4.8 μm/day), but was much slower at 19°C (2.5 μm/day). Similarly, larvae reached a mature stage more quickly when reared at 16°C, as compared to 12°C (Table 2). This phenomenon has been observed in other molluscs (Ansell 1961, Bayne 1965, Pechenik 1980).

It appears that the optimal temperature for rearing *C. hastata* larvae in terms of growth and survival is between 12 and 16°C. In the natural environment, this is probably the temperature range that most *C. hastata* larvae encounter. Although no studies have been done on distribu-

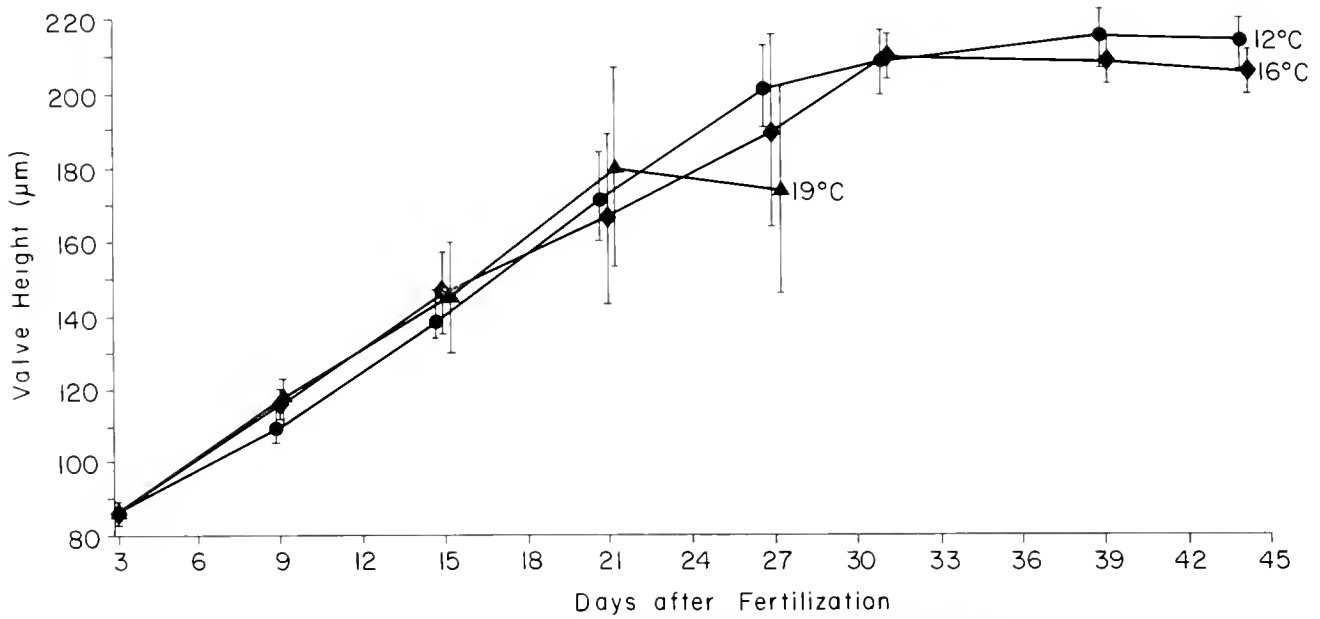


Figure 5. Valve heights of *Chlamys hastata* larvae reared at different temperatures.

TABLE 2.

Summary of larval life of *Chlamys hastata* held at 12° and 16°C.

Temperature (°C)	Time when Mature (Days after Fertilization)	Time when able Metamorphose (Days after Fertilization)	Maximum Age (Days after Fertilization)
16	34	34–96	103
12	42	42–112	120

tion of scallop larvae along the west coast of British Columbia, studies on larvae of *Patinopecten yessoensis* in Japan indicate that they concentrate in the upper 5–15 m of the water column (Ventilla 1982). *C. hastata* adults probably spawn in late summer or early fall in southern British Columbia (Bourne 1987). Assuming that *C. hastata* larvae have a similar vertical distribution as reported by Ventilla, then the temperature range that the larvae may encounter would be between 10–18°C (Hollister and Sandnes 1972, Dodimead 1984).

Growth of *C. hastata* larvae was linear during the first 20–25 days, but declined just prior to their attaining maturity (pediveliger stage). Bayne (1965) and Gerdes (1983) suggested that a decline in growth rate as the pediveliger stage is reached is caused by a decline in feeding rate owing to degeneration or decrease in size of the velum. However, the velum of *C. hastata* did not begin to show visible signs of degeneration until about 95 days after fertilization, well after shell growth had ceased, and there appeared to be no relationship between the declining rate of shell growth and the ability to feed in *C. hastata* larvae. Sprung (1984a) suggested that growth may be affected by a proportionally larger amount of energy being utilized for swimming in larger larvae. This may account for the gradual decline in growth rate noted between day 20 and day 30 but does not explain why an increase in valve length ceases altogether after day 30. Even larvae that survived as long as 100 days had the same valve length as larvae only 30 days old. It appears that a maximum size is reached and no further energy is expended in shell secretion.

Larvae reared at 12°C developed slower and reached a significantly larger maximum size than those reared at 16°C (Student's T-test; $p < 0.001$; Figure 3). An inverse relationship between valve length and developmental time also has been observed in larvae of *Mytilus edulis* (Bayne 1965), *Crepidula fornicata* (Pechenik and Lima 1984) and *C. plana* (Lima and Pechenik 1985). Bayne (1965) suggested that the time available for feeding among larvae

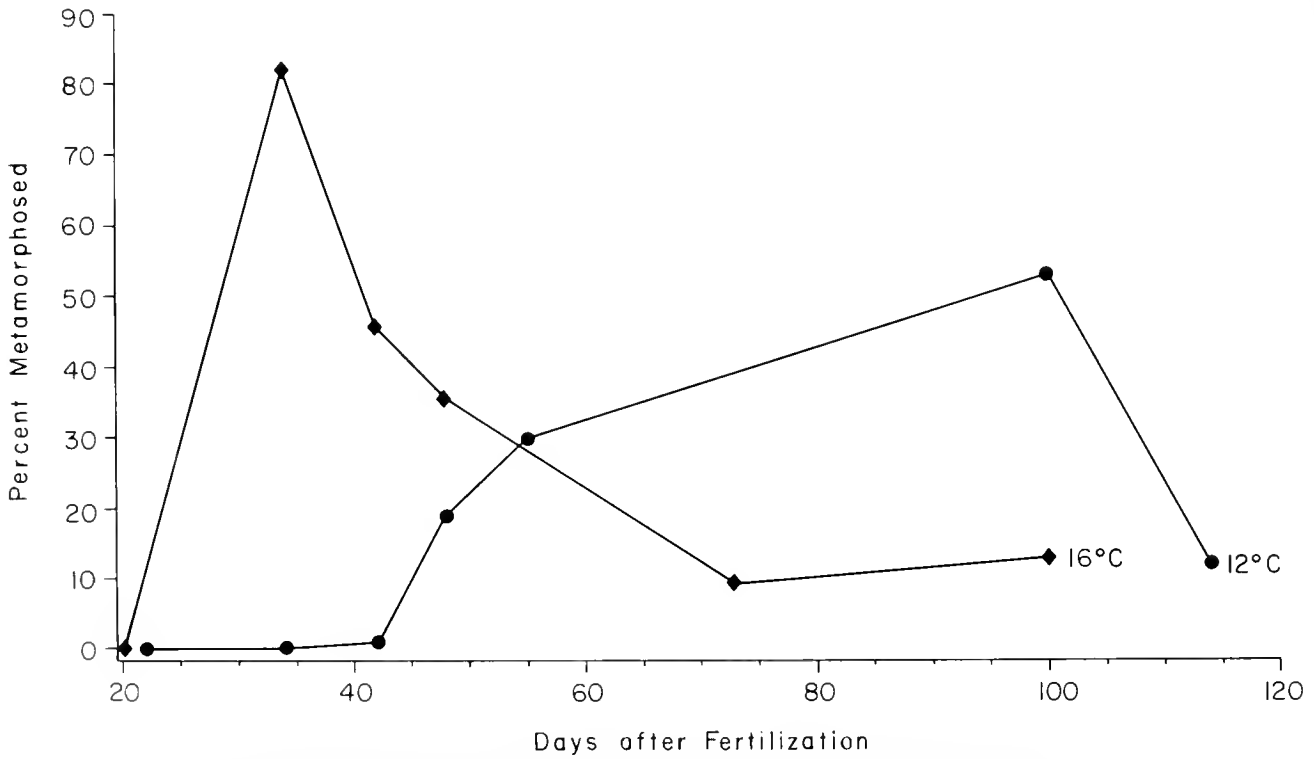


Figure 6. Percent metamorphosis of *Chlamys hastata* larvae of different ages reared at 12 and 16°C.

TABLE 3.

Percent metamorphosis of *Chlamys hastata* pediveligers 24 hours after the introduction of chemicals or substrates.

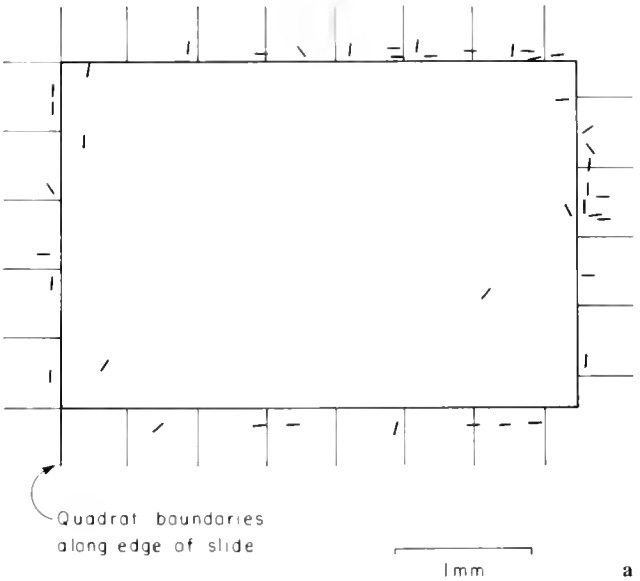
Chemical or Substrate	Number of Trials (50 larvae/trial)	% Metamorphosis
Control	2	0
GABA, 10^{-5} M	3	0
10^{-4} M	3	0
10^{-3} M	3	0
L-Dopa, 10^{-6} M	1	0
10^{-5} M	1	0
10^{-4} M	1	0
10^{-3} M	1	0
Adult Shell	2	0
Adult 'Extract'	2	0
Polypropylene Line	3	0
Fouled Surface	4	5

reared at higher temperatures was not sufficient despite the faster rate of growth and, therefore, a smaller maximum valve length was reached. However, as mentioned above, maximum valve length was reached before larvae were no longer able to feed, and so it is unlikely that the smaller size is a result of dietary constraints. Rather, the increased respiration of larvae reared at higher temperatures may not be adequately compensated by increased ingestion rate (Sprung 1984b). Thus, a greater portion of assimilated energy is used to satisfy metabolic needs rather than growth and accumulation of reserves.

TABLE 4.

Results of Wilcoxon Paired Sample Test for the effect of fouled surface or flowing seawater on percent metamorphosis of *Chlamys hastata* pediveligers.

% metamorphosis in presence or absence of fouled surfaces		% metamorphosis in presence or absence of flowing seawater	
Present	Absent	Present	Absent
53.2	26.0	45.2	2.0
14.0	2.0	26.0	6.0
10.0	0.0	33.3	2.0
30.0	11.4	5.7	0.0
12.5	6.0	40.5	0.0
2.0	2.0	6.6	0.0
2.0	0.0	29.0	0.0
4.4	0.0	11.4	0.0
2.0	0.0	53.2	12.5
9.1	0.0	14.0	2.0
13.0	0.0	10.0	0.0
59.0	5.7	20.6	0.0
40.5	6.6	43.0	0.0
		30.0	4.4
N = 13		N = 14	
H_0: % metamorphosis is independent of substrate		H_0: % metamorphosis is independent of flow	
Reject H_0, $p < 0.0001$		Reject H_0, $p < 0.001$	



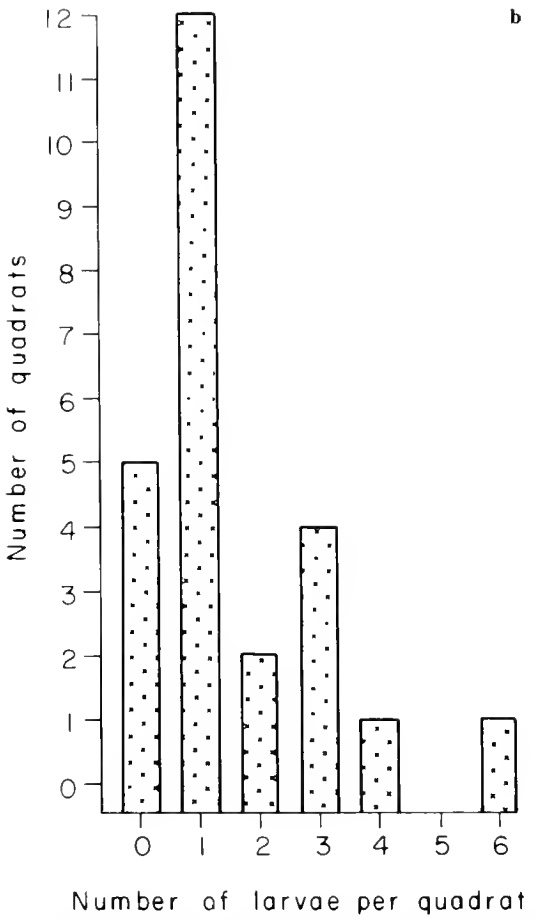


Figure 7. a) Distribution of attached and metamorphosed *Chlamys hastata* postlarvae on planar surface and edges of glass slide. b) Frequency distribution of *Chlamys hastata* postlarvae (shown by -) along edges of slide. The area along the edges of the slide wasd divided into 25 0.5 mm quadrats and the number of postlarvae per quadrat was tested for agreement with a random (Poisson) distribution using the X^2 test.

Increase in valve length corresponds to a proportional increase in valve height (1.1:1). This relationship is independent of temperature though growth rates and maximum valve length vary. Knowledge of this relationship may be a useful tool for identifying *C. hastata* larvae from plankton samples.

Metamorphosis

The ability to prolong larval life until a suitable stimulus or substrate is found has been observed in several marine invertebrate larvae (Bayne 1965, Crisp 1974, Culliney 1974, Sastry 1979, Burke 1983). In some species, if the larva does not encounter the proper stimulus over a long period of time, its "selectivity" declines and it will eventually metamorphose, presumably in the absence of the stimulus (Crisp 1974). Larvae of other species will metamorphose only if the proper stimulus is encountered or will die as larvae. In the laboratory, *M. edulis* larvae survived for up to 42 days and did not metamorphose unless a filmentous substrate was introduced to the experimental vessels (Bayne 1965). Similary, *C. hastata* larvae could survive up to 70 days after maturity was reached (12°C) and still have the capacity to metamorphose. This ability to remain physiologically ready to metamorphose for a long period of time may increase the probability of the larva encountering a suitable substrate for metamorphosis (Bayne 1965).

Surfaces covered with a film of micro-organisms are known to increase the rate of metamorphosis in larvae of *Ostrea edulis* (Cole and Knight-Jones 1949, Walne 1974), *Spirorbis borealis* (Knight-Jones 1951, Meadows and Williams 1963), and *Watersipora cucullata* (Wisely 1958). In the present study the rate of metamorphosis in *C. hastata* was higher when a fouled surface was present. No attempt was made to determine the nature of the fouled surface, but it was probably a bacterial and/or diatom film.

A flow of water appeared to stimulate settlement and metamorphosis in *C. hastata* larvae. No attempt was made to alter the type or velocity of flow and there was undoubtably considerable turbulence within the nitex cup. Movement of water over a surface has been shown to induce *Balanus balanoides* to settle on a substrate (Crisp and Meadows 1962). As well, Eyster and Pechenik (1987) observed that *M. edulis* larvae settled on substrates more readily if the water was agitated, simulating a water current. A similar situation may exist with *C. hastata* larvae where a flow of water induces larvae to begin crawling on a substrate and metamorphosis possibly is induced by the microbial layer adhering to the substrate.

C. hastata postlarvae tended to be distributed along the edges and corners of substrates rather than on other surfaces. Settlement along edges of a slide followed a random distribution (Figure 7), suggesting that larvae do not settle gregariously. Most studies examining settlement and metamorphosis in other pectinid species have focused on substrate perferences of larvae. Generally, filamentous objects, such as monofilament netting and filmentous hydroids or red algae, have induced metamorphosis in some pectinids (Motoda 1977, Allen 1979, Gruffydd and Beaumont 1972), but non-filamentous substrates have been regarded as favourable as well (Brand et al. 1980, Culliney 1974). Contour or shape of the substrate may also influence settlement and metamorphosis in *C. hastata* larvae.

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VARIABLE GROWTH RATES OF SEED CLAMS *MERCENARIA MERCENARIA* (LINNE) IN AN UPFLOW NURSERY SYSTEM AND THE ECONOMICS OF CULLING SLOW GROWING ANIMALS

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ABSTRACT The growth rates of seven separate size classes of seed clams, (*Mercenaria mercenaria*), all cohorts of a common mass spawning, were monitored weekly in a upflow nursery system from June 15 through September 9, 1986. Six of these size classes were isolated from an initial group of 750,000 0.75 mm hatchery-reared clams by passing the animals through appropriately sized mesh sieves (1.0, 1.4, and 2.0 mm) 41–60 days after spawning or 14 to 33 days after introducing the animals into the nursery system. The seventh group, comprised of the last 0.5% of the same cohort to attain 0.75 mm, was isolated with a 545 micron sieve 46 days from spawning. Each size class was held in separate passive upflow cylinders and thinned weekly to allow for maximum growth. Experimental results were placed into a cost-analysis model to compare commercial production costs with and without culling in an effort to determine if production costs could be decreased by removing slow growing animals from the production system. There were significant differences in the growth rates of certain size classes which demonstrates the ability to use current relative size to predict short term relative growth. Only size classes representing the lowest end of the size distribution (smallest 15% or less) exhibited significantly reduced rates of growth. The difference between the growth rates of fast and slow growing size classes was not great with slow growing size classes achieving field size (6 mm) only one to two weeks later than faster growing size classes. The results of the cost-analysis model indicate that removing slow growing animals from the production system would not result in a net reduction in production costs since the value of the animals discarded exceeded the savings realized by confining production to fast growing individuals.

KEY WORDS: Hard clams, *Mercenaria mercenaria*, growth, upflow system, production economics

INTRODUCTION

The culture of bivalves is characterized by high variability of growth rates among individual animals. Variable growth rates affect production efficiency by increasing handling, increasing stress to the animals associated with increased handling, and decreasing the predictability of cash flow. These problems could be reduced by identifying and removing slow growing animals from the production system. Normal operating protocols that include sorting animals by size may provide this opportunity. Using current relative size as the basis to selectively remove individuals from a production system requires that there be a significant positive correlation between relative size and future growth rate. In theory, subsequent to sorting, small animals could continue to grow at a slower rate relative to the larger animals. It is also possible that small animals could exhibit compensatory growth (Ricker 1975) and eventually catch up to larger animals, or grow at a rate equal to the larger animals.

Few studies have examined the correlation between past and future growth rates of marine bivalves. Auster and Stewart (1984) found that bay scallops (*Argopecten irradians*) exhibited compensatory growth since there was a significant negative correlation between size of one year olds and growth during the second year. Similarly, Eldridge and Eversole (1982) found that stunted (due to crowding) hard clams (*Mercenaria mercenaria*) subsequently grew at a faster rate than nonstunted animals. In another study of hard clams, Malinowski (1987a) found that there was no correlation between relative size at the end of one growing season and relative growth during the next season among four separate age classes. Newkirk (1982) monitored the growth rates of different juvenile size classes of *Ostrea edulis* for three years and found that the correlation between juvenile size and size at a later date decreased with time. He concluded that relative juvenile size was a poor predictor of adult growth.

While these studies suggest that no long term gains in production efficiency can be achieved by discarding small animals, it may still be possible to increase the short term efficiency of discrete stages of a production system, such as a nursery system where the residence time of animals is on the order of weeks rather than years, by removing slow-growing individuals.

The objective of this study was to assess the potential for using relative size as the basis to predict short term, future growth rates of juvenile hard clams (*M. mercenaria*) in an onshore, upflow nursery system and through the use of a cost-analysis model of a commercial production system, determine if overall production costs of the nursery system could be decreased by removing slow-growing size classes.

MATERIALS AND METHODS

This study was conducted in the commercial nursery production facilities of The Clam Farm, Inc., West Harbor, Fishers Island, New York, U.S.A. from June 20 through September 9, 1986. This facility has been previously described in detail (Malinowski 1987b, Malinowski and Siddall 1988). During a comparable time period in 1985, total

chlorophyll-*a* in ambient seawater entering this production facility ranged from 0.68–6.08 ug/l with a mean of 1.93 ug/l (Malinowski and Siddall 1988). Water temperature and salinity normally range from 20–24°C and 27–30 ppt. Juvenile hard clams were grown in seven 35.6 cm diameter passive upflow silos contained in a single 0.61 × 0.61 × 2.4 m plywood trough (Sensu Manzi et al. 1985). Ambient seawater flowed through the silos at a rate of approximately 16 l/m ± 1.

Hatchery-reared (Mook Sea Farms, Inc., Damariscotta, Maine, U.S.A.) seed clams (*Mercenaria mercenaria*) were introduced into the upflow system at approximately 0.75 mm (maximum dimension parallel to hinge). Size classes of animals were sorted using sieves of varying mesh sizes (1.0, 1.4, and 2.0 mm openings, corresponding to U.S. Standard Sieve Sizes of 18, 14, and 10, respectively) during the initial five weeks following introduction of the clams into the upflow system. The growth rates of these size classes were then compared. Size classes were isolated throughout the initial five week period (rather than simultaneously) to assess not only if it would be possible to identify groups of individuals that would subsequently grow at different rates, but also how long animals would need to be in the nursery system before groups exhibiting varying rates of growth could be identified.

The strategy used for sorting size classes is depicted in Figure 1. All experimental animals originated from a single mass spawning (6 males and 5 females) which produced 30 million fertilized eggs resulting in 9 million 0.75 mm animals. Two separate shipments of seed were obtained from the hatchery. The first shipment (750,000) was a random sample of the first 1.44 million to reach 0.75 mm in size. This shipment, received June 20, was separated into six size classes after growing in the upflow system for 14–32 days. The first size class was isolated by sieving a random sample of the initial hatchery group with a 1.0 mm mesh on July 3 or after the animals had been growing in the system for 14 days. Animals that passed through the mesh comprised Group 1. Four days later (July 7), the retained animals were sieved with a 1.4 mm mesh; those retained on the 1.4 mm mesh became Group 2 and those that passed through were sieved an additional time with a 1.4 mm mesh four days later (July 11). Animals that were retained and passed through the 1.4 mm mesh July 11 comprised Groups 3 and 4, respectively. On July 21, a second subsample of the original shipment from the hatchery was sieved with a 2.0 mm mesh isolating Group 6 (those animals retained on the sieve) and Group 7 (those animals that passed through the sieve). A second shipment was received from the hatchery on July 9. These animals (50,000) were the last 0.5% of the mass spawning to attain a size of 0.75 mm and comprised Group 5. Representative subsamples of each size class were maintained separately in a different silo throughout the experiment. The growth rate for each size class was monitored weekly from July 15 through September 9, 1986. Weekly samples of 100 individuals were randomly selected from each size class and measured (standard length) with vernier calipers, and total packed volume of clams in each silo was measured with a 1000 ml graduated cylinder. Total biomass was reduced to a predetermined size-specific packed volume by randomly removing a portion of the animals before returning them to a silo. The experimental groups of animals therefore contained fewer individuals as they grew during the experiment. Stocking volumes were selected to eliminate density effects and therefore allow for maximum clam growth. Stocking volumes used throughout the experiment are given in Table 1. The relative positions of the size classes within the trough were randomized each week before returning silos to the appropriate position (outlet port) within the trough.

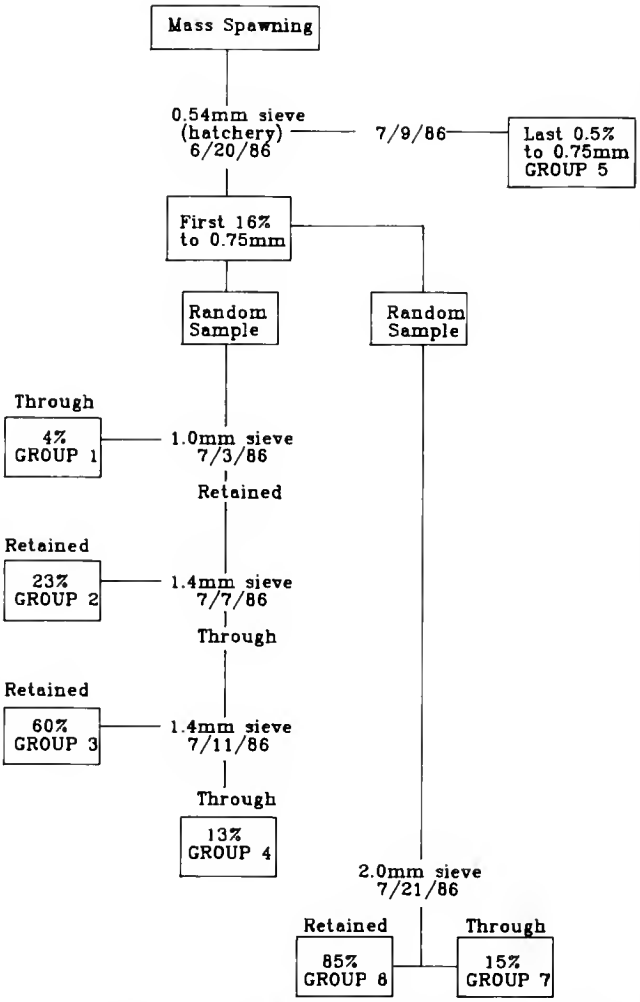

Figure 1. Description of strategy used to isolate seven experimental size classes of juvenile hard clams. Dates indicate the day of sieving with the designated sieve size. "Through" and "retained" identify whether the group was comprised of animals that were retained or passed through the sieve and percentages indicate the proportion (by number of individuals) of the initial random sample within each group.

Experimental silos were maintained on a schedule iden-

TABLE 1.

Initial stocking densities of juvenile hard clams in 35.6 cm upflow silos. Animals were removed from silos each week and thinned to the size-specific (mm, standard length) densities given below. Stocking density refers to packed volume of animals in seawater as measured with a 1000 ml graduated cylinder.

Approximate Size Range	Initial Stocking Density
1.5–2.5 mm	175 ml
2.5–3.0	350
3.0–4.0	400
>4.0	500

tical to the normal production system. The trough was drained and a high-pressure flow of ambient seawater was used to rinse the clams daily. When silos and clams were removed from the system at the end of each week, the trough, as well as all the silos, was scrubbed with detergent and a brush to remove fouling organisms.

RESULTS AND DISCUSSION

A. Growth Rates

The growth of clams within each group is depicted in Figure 2 and Table 2. Groups 1–4 and 6–7 (see Figure 1) were isolated separately from two different subsamples of the first hatchery shipment. Growth rates (comparison of slopes or increase in length through time) of Groups 1–4 as well as Groups 6 and 7 were significantly different ($p < 0.05$ and $p < 0.025$; ACOVA). Comparisons revealed that group 4 grew at a significantly lower rate ($p < 0.025$; ACOVA) than Groups 1, 2 and 3 which all grew at a similar rate ($p > 0.05$; ACOVA) and Group 5 grew significantly slower than all other groups ($p < 0.0005$; ACOVA).

Weekly increases in packed wet volume are presented in Table 3. Since weekly biomass increases are characteristically size-specific for hard clams grown in upflow nursery systems (Malinowski 1987b), the data are presented in size class (rather than time) intervals. Between-group variation in weekly biomass increases generally coincided with observed differences in individual clam growth. Weekly increases in biomass for Group 4 were less than Groups 1, 2, and 3 and increases for Group 7 were less than Group 6.

There was no evidence of compensatory growth since none of the initially slow growing groups subsequently grew at a faster rate than the faster growing animals. Almost immediately after being introduced into the upflow system, individual clams began to exhibit highly variable growth rates. For the majority of animals, however, there was no short term (within a single growing season) correlation between past and future growth rates. Only a small percentage of animals representing the lowest end of the size distribution continued to grow slowly. Increasing the time animals were allowed to grow in the culture system

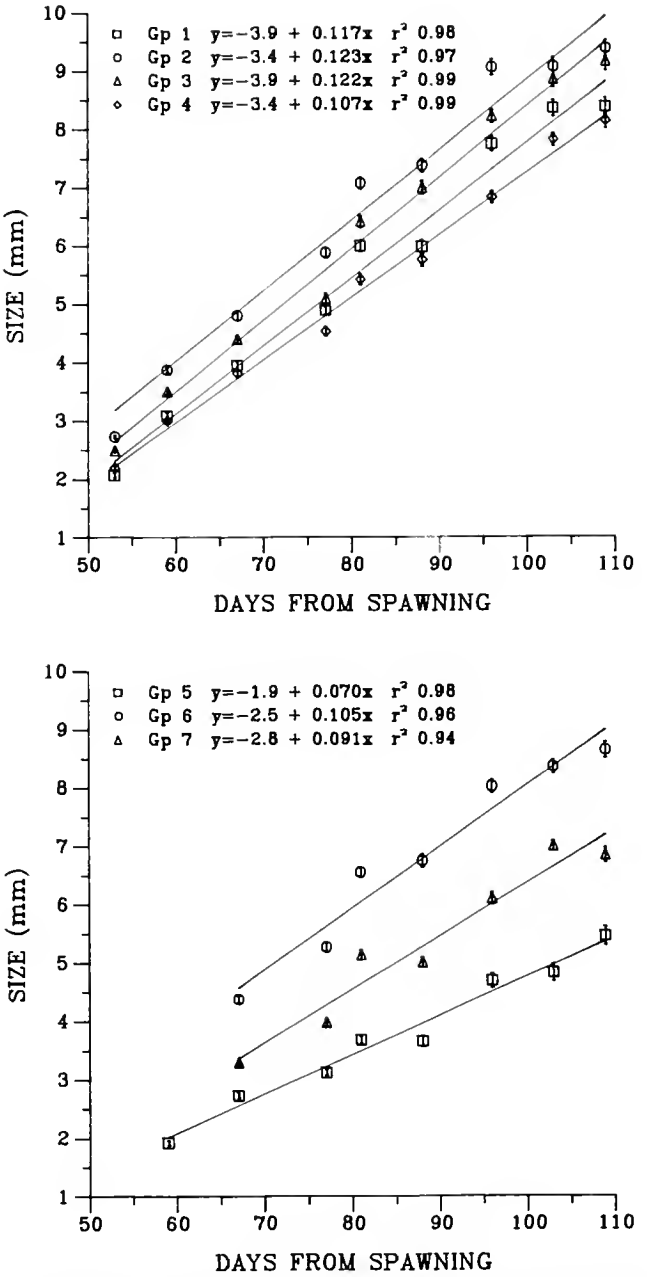

Figure 2. Growth of seven different size classes of juvenile hard clams, *M. mercenaria*, in a commercial upflow nursery system. Group (Gp) corresponds to the groups identified in Figure 1. Data points represent the mean (±SE) for each weekly sample (n = 100).

prior to sorting, increased the ability to identify size classes that would continue to grow slow. Groups 1, 2, 3, and 4 were isolated from the same random sample of the first hatchery group (see Figure 1). Group 1, isolated 14 days after the hatchery group was introduced into the nursery system, was representative of the smallest 3.8% of the first hatchery group at that time. It subsequently grew at a rate that was similar to Groups 2 and 3 ($p > 0.05$; ACOVA). It was not possible to identify a group that exhibited a correlation between relative size and future relative growth until

TABLE 2.

Final mean sizes (standard length) and growth rates of seven size classes of juvenile hard clams held in passive upflow silos (see Figure 1 for a description of the groups). Clams were measured weekly (n = 100) from July 15–September 9, 1986. The dates of initial measurements were July 15 for Groups 1–4, July 21 for Group 5, and July 29 for Groups 6–7.

Group	Initial Mean Size	Final Mean Size	Days	Mean Growth Rate (microns/day)	Mean Growth Rate[1] (microns/day)
1	2.1	8.4	56	112.5	107.1
2	2.7	9.4	56	119.1	109.5
3	2.5	9.2	56	118.9	114.3
4	2.2	8.1	56	106.1	102.4
5	1.9	5.4	50	70.0	64.3
6	4.4	8.6	42	101.7	101.7
7	3.3	6.8	42	84.5	84.5

[1] For the period July 29 through September 9.

22 days after the animals were introduced into the nursery (Group 4) and at that time, only a small proportion of the total cohort (the smallest 13% at that time) could be identified as slow growing. After 33 days, a 2.0 mm sieve was used to separate a second random sample of the first hatchery group into two size classes. The smaller size class (Group 7) grew at a significantly slower rate than the larger size class (Group 6) but again, represented only a small percentage of the size distribution (the smallest 15% at that time). The difference between the rates of growth of Groups 6 and 7 were greater than the differences observed between Groups 4 and 1, 2, and 3 (Table 3).

There is a tendency in the bivalve culture industry for growers to prefer animals that have displayed the fastest growth rates in hatchery and/or nursery systems. The rate of growth of Group 5 (the slowest growing individuals of the cohort in the hatchery) was significantly slower than all other experimental groups ($p < 0.005$; ACOVA). However, since this group was comprised of the smallest 0.5% of the size distribution of animals resulting from the mass spawning and growth rates of only two hatchery groups were compared, this study lacks the resolution necessary to determine if a correlation exists between relative growth in the hatchery and relative growth during the subsequent, nursery production stage for a meaningful proportion of the cohort.

Variability of growth rates of individual clams held in nursery systems could be due to a variety of both biological

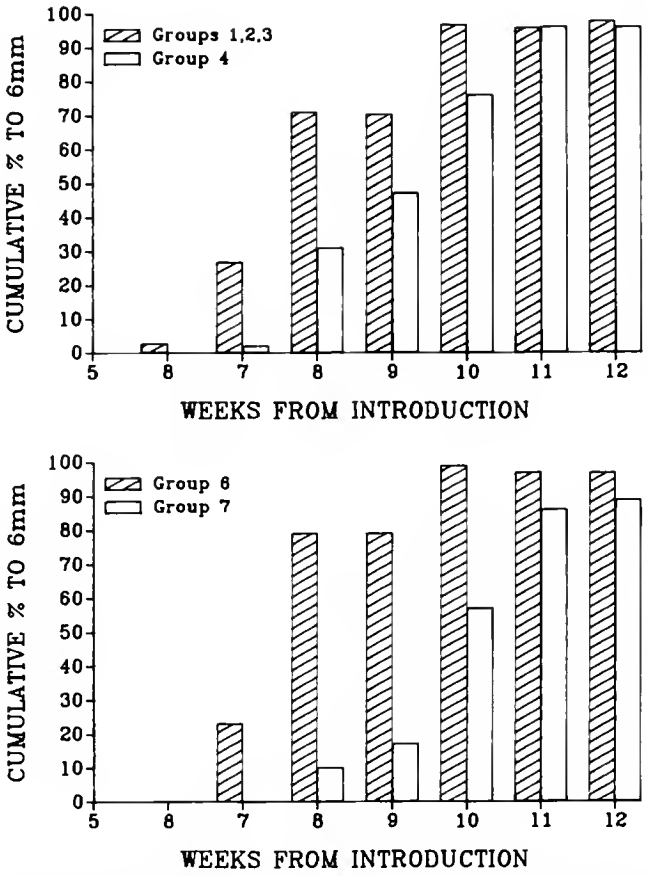

Figure 3. The time required for individuals within various groups (see Figure 1) of juvenile hard clams to attain field planting size (6 mm). Clams were introduced into the nursery system 28 days after spawning.

TABLE 3.

Percent weekly increase in packed wet volume of seven size classes of juvenile hard clams held in passive upflow silos. Data are presented in size rather than time intervals to correct for the size dependent relationship between volumetric increase and clam size.

	Approximate Size Class (mm)					
Group	3–4	4–5	5–6	6–7	7–8	Mean
1	103	86	80	52	46	73
2	78	81	75	50	54	68
3	83	83	80	52	58	71
4	83	71	55	48	52	62
5	60	54	—	—	—	57
6	77	81	75	52	48	67
7	29	77	52	50	—	52

TABLE 4.

Estimated production costs of rearing 1,000,000 6 mm hard clams with and without culling in the upflow nursery system of The Clam Farm, Inc., Fishers Island, NY. For the culling strategy Group 4 (see Figure 1) has been removed. Initial costs for hatchery reared seed (0.75 mm) are estimated to be $2.50/1,000. See text for further details.

A. Typical production—without culling

Week	Clams in System ($\times 10^3$)	Silos	S	L	E	O	Weekly Cost/clam ($\$ \times 10^{-2}$)	Accumulated Cost/clam ($\$ \times 10^{-2}$)	Clams Planted	Total Cost
1	1,000	3	5%	15	3	3	.0020	.2520		
2	1,000	4	7	20	4	3	.0027	.2548		
3	1,000	7	12	35	7	6	.0048	.2596		
4	1,000	13	23	65	13	11	.0089	.2686		
5	1,000	27	48	135	28	23	.0186	.2872		
6	1,000	36	64	180	37	31	.0248	.3120	19000	59
7	981	39	69	195	40	33	.0274	.3394	208000	706
8	773	34	60	170	35	29	.0303	.3697	457000	1690
9	316	14	25	70	14	12	.0305	.4002	68000	272
10	248	11	19	55	11	9	.0305	.4308	203000	875
11	45	2	3	10	2	2	.0306	.4615	25000	115
12	20	1	1	5	1	1	.0344	.4959	20000	99
									TOTAL	$3817

B. Hypothetical production—with culling

Week	Clams in System ($\times 10^3$)	Silos	S	L	E	O	Weekly Cost/clam ($\$ \times 10^{-2}$)	Accumulated Cost/clam ($\$ \times 10^{-2}$)	Clams Planted	Total Cost
1	1,145	3	5%	15	3	3	.0018	.2518		
2	1,145	5	8	25	5	4	.0030	.2548		
3	1,145	9	16	45	9	8	.0054	.2602		
4	1,000	13	23	65	13	11	.0089	.2691		
5	1,000	27	48	135	28	23	.0186	.2878		
6	1,000	36	64	180	37	31	.0248	.3126	24000	75
7	976	39	69	195	40	33	.0275	.3401	249000	847
8	727	32	57	160	33	27	.0303	.3705	470000	1741
9	257	11	19	55	11	9	.0295	.4000	53000	212
10	204	9	16	45	9	8	.0304	.4304	184000	792
11	20	1	1	5	1	1	.0344	.4648	20000	93
									TOTAL	$3760
									Difference (A–B)	$56
									Value of clams discarded	$377

and physical factors. Size of individuals at a point in time will be the result of a combination of factors such as genetics, periodic rather than continuous growth, differential stress and environmental variability. For example, in a study of juvenile hard clam (*M. mercenaria*) growth in a raceway nursery system, Hadley and Manzi (1984) documented a significant effect of position within raceways on clam growth. Variability within individual upflow silos has not been investigated but is certainly possible. The degree to which size is a function of factors other than genetics, such as an artifact of the nursery system environment, will determine how accurately future growth may be predicted from relative size. The results of this study suggest that most variability is due to extrinsic factors and only the extreme lower end of the size distribution, isolated after an appropriate time interval, will continue to grow at a slow rate.

B. Economics of Culling

The potential for increasing production efficiency by removing slow-growing animals is dependent upon the ability to identify slow growing animals and the economics of the production facility. Theoretically, production costs per clam could be reduced by removing slow growers if culling results in an increase in the number of clams produced per unit time (slow growing animals replaced with faster growing animals) or a decrease in the average residence time of animals in the production system.

The upflow nursery system of The Clam Farm, Inc. is used to grow animals to 6 mm before field planting. An important, practical consideration is the relative time it takes fast and slow growing size classes to achieve field-planting size (see Figure 3). The majority of animals in group 4 (the slow growing group isolated with the 1.4 mm

mesh) attain 6 mm just one to two weeks later than the faster growing groups. Production could not be increased by replacing this size class with a new hatchery group since an initial growth period in the nursery system of 22 days was required before the size class could be identified. The difference between the growth rates of Groups 6 and 7 (isolated with the 2.0 mm mesh) was greater, and although the experiment was terminated before all the clams in Group 7 attained 6 mm, most (>85%) clams in Group 7 grew to a size of 6 mm just one to two weeks later than the rest of the animals (see Figure 3). In this case, 32 days of initial growth in the nursery system were required before the slow growing group could be identified.

Removing a slow growing size class does decrease the average residence time of animals in the nursery system and confining production to fast growing animals will reduce costs. The net savings realized, however, will be the difference between the reduced costs and the value of the animals that are discarded. Given that individuals within a single hatchery group take varying amounts of time to achieve field size (see Figure 3), the total costs of growing a group of hatchery-reared seed in a nursery system to a size that can be planted in the field can be simplistically described as

$$C = I + \Sigma N_t(V_1 + V_2 + \ldots V_t)$$

where C = total cost of growing an entire cohort to field size, I = initial costs for hatchery-reared seed, N = number of animals to attain field size, V = production costs per clam and t = time (weeks in this case). Production costs per clam (V) accumulate incrementally as a function of the operating costs of a nursery. Assuming the nursery system uses ambient seawater and space not utilized by one cohort is used by another, the incremental production costs per clam (V) can be described as

$$V_t = [(L + E + O)(S_t)]/T_t$$

where L, E and O are the weekly labor, electricity, and overhead costs for operating the entire nursery system, S = the percent of the total nursery system occupied by a cohort, and T = the total number of individuals of the cohort in the nursery system.

This model was used to compare the costs of producing one million 6 mm hard clam seed with and without culling to determine if net savings could be realized (see Table 4). The analyses assumed 100% survival (survival affects total cost but not relative costs with and without culling) and the system was operating at capacity (space not utilized by an experimental cohort was utilized by another cohort). In decreasing the average residence time of animals in the nursery system, culling changes the pattern of when individuals of a cohort achieve field size. This information (N_t in the above model) was derived from Figure 3. For the outdoor, seasonally operated nursery system of The Clam Farm, Inc., estimates for L = $280/week, E = $58/week and O = $48/week to operate the system when it is filled to capacity (56 silos). Labor costs were based on an estimate of 35 hours per week at $8.00/hr. and estimates for electricity and overhead were derived by dividing the actual costs for these items during the period 1983–1987 by the total number of weeks in production (initial construction costs for the nursery system are included in the estimate of overhead).

Removing slow growing groups reduces total production costs since a larger proportion of the cohort achieve 6 mm early, when costs per clam are less. The differences in the total production costs with and without the culling strategy, however, were slight (1.5% and 2% less when groups 4 and 7 were removed) and considering that the value of the discarded groups were much greater, a net loss would be incurred by employing the culling strategies.

While it is possible to use current relative size to predict future growth rates, only a small proportion of a cohort can be identified as slow growing. Since prolonged periods of initial growth in the nursery system are required before slow growing size classes can be isolated and there is only a slight difference between the time it takes slow and fast growing animals to attain field size, it does not appear possible to realize net savings in production costs by discarding slow growing animals.

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DESCRIPTIONS OF MACROSCOPIC BANDING PATTERNS IN SECTIONED POLISHED SHELLS OF *MERCENARIA MERCENARIA* FROM SOUTHERN NEW JERSEY*

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ABSTRACT Internal macroscopic bands in sectioned, polished shells of hard clams, *Mercenaria mercenaria* (Linné), from southern New Jersey showed a seasonal pattern consisting of: (1) a wide light-colored spring band; (2) a wide dark summer band; (3) a wide light fall band; (4) a thin dark slow-growth band, or 'break,' deposited in winter. These bands were usually visible in the middle and outer shell layers from the umbo to the ventral margin. The pattern was variable from individual to individual, and was particularly inconsistent for the first 2 years of growth. Of 550 specimens examined, 83% had at least three of the above four seasonal bands identifiable for each of the first 5 years of growth. All four seasons of the annual pattern were not easily distinguishable in most specimens after the first 5 to 10 years of growth because shell growth rate declines, thus compressing the bands into a narrower portion of the shell. Nonetheless, alternating light and dark bands were easily visible in some individuals >20 years old. The annual pattern for *M. mercenaria* from southern New Jersey was very similar to that reported by others from Virginia and North Carolina, except that a winter 'break' was more consistently evident in specimens from New Jersey.

KEY WORDS: *Mercenaria*, hard clam, growth, internal shell band, New Jersey

INTRODUCTION

Growth patterns within molluscan bivalve shells have been used in various ecological, paleontological and archeological studies (for review see Lutz and Rhoads 1980). Growth increments thus far described range from microgrowth lines forming with approximately daily periodicity (e.g., Barker 1964, Evans 1975, Kennish 1980) to bands forming annually that are macroscopically visible in sectioned, polished valves (e.g., Lutz 1976, Peterson et al. 1983, 1985). Clearly there is great potential for use of these records of growth changes contained within the molluscan shell. However, caution has been urged with regard to using shell growth patterns for ecological and other studies until particular patterns for the species being studied have been well assessed (Jones 1981, Peterson et al. 1983, Fritz and Lutz 1986). Only if a specific pattern is adequately documented (i.e., determined by adequate tests that the pattern is repeating and periodic) and described, can it be useful in such studies.

The hard clam, *Mercenaria mercenaria*, has been the subject of numerous studies on internal shell growth patterns. Microgrowth patterns revealed in acetate peel replicas of polished and etched radial sections (Kennish 1980), or polished radial thin sections of shell valves, have been described photographically in the literature using specimens of *M. mercenaria* from New England (Pannella and MacClintock 1968, Rhoads and Pannella 1970), New Jersey (Kennish and Olsson 1975, Kennish 1980), and Virginia (Fritz and Haven 1983). Macroscopic patterns visible in sectioned, polished valves of this species, however, only have been described photographically in the literature for specimens from North Carolina (Peterson et al. 1983). The presence of a distinct macroscopic seasonal banding pattern has been well-established (i.e., documented) in studies ranging from Massachusetts to Georgia (Pannella and MacClintock 1968, Rhoads and Pannella 1970, Kennish and Olsson 1975, Clark 1979, Kennish 1980, Fritz and Haven 1983, Peterson et al. 1983, 1985), but the macroscopic banding patterns have not been photographically described for most areas. Photographs of microgrowth patterns can be potentially useful for describing macroscopic patterns (see discussion in Fritz and Haven 1983). However, most of the published photographs of microgrowth patterns for *M. mercenaria* are of only a small portion of the shell so a complete annual macroscopic pattern is not easily discernable.

It is important that adequate photographic descriptions of the banding patterns from different areas be published because written descriptions are not sufficient for unambiguous identification of various features. Furthermore, because of the relative ease of processing sectioned, polished valves (compared to preparation and examination of acetate peels or thin sections), this methodology may be most appropriate for some studies. Peterson et al. (1983) suggested that concern over the lack of controlled tests documenting banding patterns may be partly responsible for the lack of

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widespread use of such shell information by population biologists. We suggest that lack of adequate descriptions of banding patterns also has been a factor. With respect to the present study, we emphasize that repeating annual internal shell banding patterns have been well documented in *M. mercenaria* from the U.S. Atlantic Coast (see references above). However, photographic descriptions of the macroscopic patterns from most areas have not been published and these descriptions are a necessary basis for further work on aging and growth. The purpose of the present report is to provide photographic descriptions of the seasonal macroscopic banding patterns in sectioned, polished shells of *M. mercenaria* from southern New Jersey.

METHODS

A total of 550 living specimens of *M. mercenaria* was collected from natural populations inhabiting a wide range of sediment types in Great Sound, a coastal lagoon in southern New Jersey (between 39°00′ and 39°10′ north latitude and 74°40′ and 74°50′ west longitude; see Ashley and Grizzle 1988, and other reports in same volume, for descriptions of Great Sound), and adjacent tidal channels in October 1985, and April and September 1986. Thus, individuals were available from early spring when the growing season had just begun, and late summer when water temperatures had started to drop and the fall fast-growth period was beginning.

All specimens were killed with steam in an autoclave, sectioned along the maximum axis of growth (see Figure 1 in Rhoads and Pannella 1970) on a carbide blade table saw, and wet polished using 200 and 600 grit paper on grinding wheels. Each polished valve was examined with the unaided eye and under a stereomicroscope at 10×. All photographs (Figure 1) were taken using a 35 mm camera attached to a stereomicroscope, except 1A which was taken using a close-up lens.

RESULTS

The various banding patterns associated with different seasons and different ages of clams are shown in Figure 1. The annual seasonal banding pattern was:

1. A wide light-colored spring band;
2. A wide dark summer band;
3. A wide light fall band; and
4. A narrow dark slow-growth band, or 'break,' deposited in winter (Figure 1A, this clam was harvested on 15 October 1985).

These bands usually occurred in the middle and outer shell layers and the overall pattern was most consistently evident for years 3 through 6.

The annual pattern was not easily identifiable on some clams and there was wide variability among individuals. Of the 550 clams examined, 83% had at least three of the four seasonal bands identifiable in each of the first 5 years of growth (except year 1). The descriptions herein are primarily only for the first 5 years of growth; and all individuals in Figure 1 were less than 6 years old, except the specimen in 1B and C. After the first 5 to 10 years shell growth rate usually decreases, and banding patterns are thus compressed within a narrower area of the shell making macroscopic discernment of all four seasonal bands difficult. However, alternating light and dark bands which would at least allow determination of annual periodicities were easily visible in some clams >20 years old, and in most individuals for up to the first 10–15 years of growth.

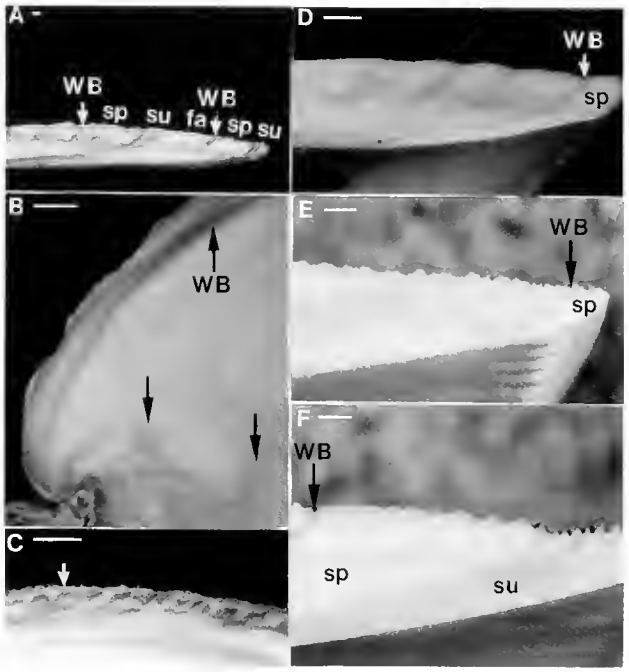

Figure 1. Sectioned, polished shell valves of *Mercenaria mercenaria* from Great Sound in southern New Jersey. WB = winter break, sp = spring, su = summer, fa = fall. Bar in each photograph shows 1 mm. A. Specimen collected on 15 October 1985 showing two annual banding patterns including the fifth and sixth (the last) winter breaks. B. Annual pattern for first year, and part of umbonal area, in a specimen collected on 5 September 1986; arrows in umbonal area indicate first two annual dark summer bands. C. The second annual band from the specimen in B; arrow indicates beginning of wide dark summer band. D. Specimen harvested on 20 April 1986 showing early spring growth at shell margin, and the third (the last) winter break. E. Specimen harvested on 20 April 1986 showing early spring growth following the fifth (the last) winter break. F. Spring-summer growth following the fifth (the last) winter break in specimen harvested on 5 September 1986.

Patterns of growth up to and including deposition of the first winter break (i.e., the first ~6 months of growth; assuming mid-summer settlement, see Carriker 1961) were especially variable, typically showing no discernable pattern and an indistinct winter break. In particular, a definite narrow winter break preceded by a light fall-growth band, was not usually evident. The "WB" in Figure 1B denotes the area of the first winter break. It was typically identified by following the first wide dark band from the umbonal area (arrows in 1B show first two dark bands in the um-

bonal area) to the point where it merged with the outermost dark band in the lower portion of the shell.

Growth patterns were also often indistinct for year 2 when the absolute annual shell growth increment was usually greatest (Grizzle 1988). The arrow in 1C indicates the beginning of a dark band in year 2 which continues into a light-colored (probably fall growth) area, but there is no distinct winter break. In many specimens the pattern for the second year was particularly anomalous in that a distinct wide dark summer band was not conspicuous. A wide dark band for year 2 was usually visible in the umbonal area (see arrows in 1B), but the corresponding pattern in other portions of the shell was often indistinct.

Figures 1D and E show specimens harvested on 20 April, with the third and fifth winter breaks (their last), respectively, labelled. The narrow light area at the end of the shell indicates each clam had just begun its spring fast-growth period. Such individuals had a light-colored lip around the outer edge of their valves easily visible in the field when harvested. Figure 1F shows a specimen harvested on 5 September; its fifth (and last) winter break is labelled "WB." The dark wide summer band is clearly visible.

Alternating light and dark bands were almost always visible in the umbonal area (Figure 1B), and they usually corresponded to patterns in the outer portion of the shell (but see comments above regarding year 2). Hence, patterns in the umbonal area were used as a check for patterns in the lower portion of the shell.

DISCUSSION

It is difficult to compare the banding patterns herein with those described by other workers because most previous work was based on examination of thin sections or acetate peels where designations such as "light" and "dark" were not always made (but see discussion of Fritz and Haven 1983 below). Furthermore, whether or not a band is light or dark depends on the preparation technique used (see discussion in Fritz and Haven 1983) and method of viewing. Thus, written descriptions potentially can be misleading. However, the one published photograph of polished sections (Peterson et al. 1983), and a set of photographs of acetate peels (Fritz and Haven 1983), with accompanying written descriptions, are quite useful for comparison with patterns reported herein.

Four polished, sectioned valves from North Carolina *M. mercenaria* are shown in Peterson et al. (1983). In these specimens external ink marks put on the shell margin several times during the 4+ year study were compared with internal patterns revealed in the sectioned shells. The internal macroscopic banding pattern consistently (n = 152 clams) showed a dark band formed between May and October, and a light band from November to April. Other than the apparent absence of a dark winter line, the banding pattern described for these clams form North Carolina is similar to that reported herein for specimens from New Jersey.

Of the published photographs of thin sections or acetate peels, those in Fritz and Haven (1983) of clams from Chesapeake Bay, Virginia appear to be most useful for comparison to polished sections. Their photographs show the outer 10+ mm of the sectioned shell, which corresponded to about 1 year of growth. The general pattern revealed for polished sections (but shown in reverse in their photos because they were peels viewed and photographed using transmitted light; see above) was a light wide band in spring, and a dark wide band in summer (which corresponded to slower growth and water temperatures >25°C), followed by a wide light band in fall (which corresponded to increased growth rates). In some animals a dark narrow winter break separated the light fast-growth bands of fall and spring, but this did not always occur. This pattern (when the winter break did not occur) was very similar to that reported by Clark (1979) for clams from Georgia. Hence, as in North Carolina (Peterson et al. 1983) and New Jersey (present study) a wide dark summer band was formed, and a wide light band occurred in the cooler spring and fall months. However, whereas no mention was made of a dark winter break by Peterson et al. (1983), some of the specimens from Virginia showed this pattern as did most of the specimens from New Jersey in the present study. Apparently the latitudinal gradient, which reflects differences in winter temperature extremes, is reflected in these differences in winter banding patterns.

These findings appear to be contradictory to previous data on *Mercenaria mercenaria* from the northeastern United States, but because of the lack of photographic descriptions of the banding patterns it is difficult to adequately compare macroscopic patterns. The apparent contradiction concerns the timing of deposition of a "dark" band. Pannella and MacClintock (1968), Rhoads and Pannella (1970), and Kennish and Olsson (1975) studying *M. mercenaria* from Massachusetts to New Jersey all reported decreased daily growth increments as water temperatures decreased in the winter, and a distinct winter slow-growth "break" or band which was presumably dark in a polished section (Kennish and Olsson 1975 described it as "dark."). However, "heat-shock" and "thermal-shock" breaks were also described by Kennish and Olsson (1975) as similar to the winter "freeze-shock" break. Thus, "dark" bands have been reported from northern specimens as occurring in summer and winter. The present study and data in Fritz and Haven (1983) discussed above indicate that the major difference between the two "dark" bands is their width. The summer band is much wider than the winter band, so the winter band is perhaps better described as a dark "break" (see above). Furthermore, because the seasonal banding patterns are quite variable from individual to individual it is best to always look for the particular order of seasonal bands that occurs in the area of study. For

example, one of us (REG) used the winter break as the annual marker for determining growth rates for the specimens described herein (Grizzle 1988). In these growth studies the winter break was always verified by making sure that the dark wide summer band and the light fall band preceded it, and a light spring band followed it. In some individuals all bands were not present, or at least not clearly visible each year, so there was some ambiguity in the identification of seasonal patterns during some years. However, as noted above, in 83% of the specimens at least three of the four seasonal bands for each of the first five years (except year 1) were identifiable.

Clark and Lutz (1982) described banding pattern differences among *Mercenaria mercenaraia* collected at monthly to bimonthly intervals from sites in Maine, New Jersey, North Carolina and Georgia. Only an abstract has been published, so no detailed comparison can be made. However, they noted in comparing individuals from North Carolina and New Jersey that ". . . features characteristic of winter in one locality can occur in summer in the other." This suggests that local variations can be extreme, when considering the fact that the seasonal patterns reported herein were very similar to that reported by Peterson et al. (1983) for specimens from North Carolina. Hence, the pattern reported herein for *M. mercenaria* from southern New Jersey may not be the only one possible for New Jersey specimens.

Geographic differences in banding patterns may reflect differences in ambient water temperature fluctuations on a seasonal scale, particularly summer and winter extremes (Lutz and Rhoads 1980, Fritz and Haven 1983). Temperature is unquestionably a major determinant of growth rates, and seasonal changes reflect its influence (Ansell 1968). Therefore, comparative studies such as those conducted by Clark and Lutz (1982) are needed to provide adequate documentation and photographic descriptions of banding patterns. Only after such information is gathered on a species-by-species basis can growth information contained within molluscan shells be effectively used.

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REPRODUCTION OF DIFFERENT STOCKS OF *MERCENARIA MERCENARIA**

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ABSTRACT Juvenile *Mercenaria mercenaria*, from Aquaculture Research Corporation (ARC) in Dennis, Massachusetts, a South Carolina wildstock (SCW) and a cross of the two (ARC × SCW) were planted in the Colleton River, South Carolina in 1983. Subsamples were collected from July 1984 to August 1985 and histologically examined. Sexual maturity occurred at 20–25 mm shell length (SL) in SCW and 30–35 mm SL in ARC × SCW and ARC stocks. Significant differences ($p \leq 0.01$) were detected among stocks, months and the interaction in level of spawning condition. ARC stock showed distinct spawning peaks in April and August, with a smaller peak in December while the SCW stock spawned only in March and July. Offspring of the ARC × SCW cross exhibited an intermediate spawning pattern. ARC × SCW stock shed significantly ($p \leq 0.05$) more eggs than either parental stock, but there were no statistical differences between parental stocks. Egg diameter was significantly different ($p \leq 0.05$) among stocks, but the mean difference was < 1 μm. Egg size decreased significantly ($p \leq 0.05$) with spawning trial. Female SCW and ARC × SCW spawned significantly ($p \leq 0.05$) more times than females in the ARC stock. SCW stock had the highest oocyte area/follicle area (follicular condition) after 10 spawning trials indicating a capability to continue spawning. SCW and ARC × SCW exhibited similar spawning peaks and recovery periods during the spawning trials. A sex ratio of 2.4:1.0 (f:m) and three hermaphrodites were observed in 45 clams spawned in the ARC stock.

KEY WORDS: *Mercenaria*, hard clams, gametogenesis, spawning, stocks, fecundity

INTRODUCTION

The hard clam, *Mercenaria mercenaria* (L.), is distributed from the Gulf of St. Lawrence to the Gulf of Mexico from a depth of 15 m to the intertidal zone (Menzel 1970). Hard clam beds have been established on the United States west coast, in the British Isles and parts of France (Ansell 1968).

In the Northeast, a management strategy referred to as spawner transplants involves harvesting chowder size hard clams (>80 mm SL) in June or July from cooler waters and planting them in warmer, more desirable beds to extend the spawning season. Kassner and Malouf (1982), however, found that the gametogenic cycle of transplant and native hard clams in Great South Bay, New York, were similar and that transplanting did not extend the spawning season. Ropes (1971) noted that hard clams from areas north of Chincoteague Bay, Maryland, spawned at lower temperatures and suggested a physiological reason to account for this difference.

Newkirk (1980) cited that H. H. Haskin maintained in Delaware Bay lines from geographically isolated stocks of *Crassostrea virginica* and, after several generations, these lines continued to show temperature threshold differences for gametogenesis. Differences in conditioning periods have been attributed to genetic factors in *C. gigas* (Lannan et al. 1980). Dalton and Menzel (1983) suggested, based on work with *M. mercenaria* and *M. campechiensis* hybrids, that the gametogenic cycle is under genetic control. Observed differences in the spawning peaks in *M. mercenaria* populations indicate that difference stocks occur along the Atlantic seaboard of North America (Loosanoff 1937, Porter 1964, Keck et al. 1975, Eversole et al. 1980, 1984, Pline 1984, Manzi et al. 1985).

Genetic factors affecting gametogenesis and fecundity are an integral part of breeding programs designed to improve cultured stocks. Application of reproductive genetics in hard clams can be found in the works of Bricelj (1979), and Kraeuter et al. (1972), which reported variable egg sizes and increased survival of larvae with larger eggs. Large eggs would be desirable, whether it resulted from a heritable trait or as a result of optimum conditioning. The present study was undertaken to evaluate spawning cycle, differentiation, sexual maturity, fecundity, egg size and response to repeated spawning stimuli, among stocks of hard clams selected for an applied breeding program (for a summary of the breeding program see Manzi et al. 1988a, b).

MATERIALS AND METHODS

Field Evaluation

Progeny from crosses involving hard clams from Aquaculture Research Corporation (ARC) in Dennis, Massachusetts, a South Carolina wildstock (SCW) from the Charleston area and both sites (ARC × SCW) were held at

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the South Carolina Marine Resources Division field station on Folly River until large enough to plant. Juvenile clams from ARC (8.0 mm shell length, SL), SCW (7.5 mm SL) and the cross of ARC × SCW (7.5 mm SL) were planted in sediment-filled trays (Manzi et al. 1981) in the Colleton River at the Waddell Mariculture Center in early summer 1983. In May 1985, the SCW was moved back to Folly River for further breeding experiments.

Random samples of clams (n = 20) of each cross were collected from July 1984 to August 1984 and stored in 10% buffered formalin seawater until analysis. Shell measurements were taken prior to histological preparation. Ventral portion of the clam's visceral mass was excised, embedded and sectioned at 10 μm before staining with Harris' hematoxylin and eosin Y solutions (Davenport 1960). The stages of gonadal development scored included: undifferentiated gonads, having no trace of secondary sexual products; male active, gonads with sperm cells; male ripe and spawning, gonads >75% lumen filled with sperm; female active, gonads having secondary oocytes present; and female ripe and spawning, gonads were composed of >25% total area secondary oocytes.

Differentiated and spawning condition of the gonad was numerically described for statistical analysis. Initially, all gonads were assigned either a value of zero, if the gonad was undifferentiated, or one, if it exhibited signs of sexual differentiation. These scores were then used to test the extent of gonad differentiation with analysis of variance using sample month, stock and the interaction to construct a general linear model (SAS 1985). Sexually differentiated individuals were further described with a separate rating of gonad activity (spawning condition). One was assigned to those differentiated gonads that were ripe and spawning while active gonads received a value of zero. Analysis of variance using the same model was used to detect differences in spawning condition among treatments and their interaction. Monthly levels of differentiation and spawning condition for each stock tested positively for normalcy.

Laboratory Spawning Trials

Adult clams (n = 100) from the ARC, SCW and ARC × SCW were held under conditions of 19°C and fed 300 l/day of a mixture of *Isochrysis galbana* (Tahitian isolate), *Chaetoceros gracilis* and *Platymonas* sp. for 30 days (Dec 23, 1985–Jan 23, 1986). Random subsamples of 45 clams from each cross were then selected for spawning, measured and numbered.

Spawning was attempted every three days for a period of 30 days or 10 spawning trials. Clams in individual vessels were induced to spawn by thermal induction (23–30°C) and the introduction of pasteurized sperm (Castagna and Kraeuter 1981). This process was repeated four times per trial. Number and sex of spawners were recorded. Eggs were collected by screening (20 μm) and fixed in a 10% formalin seawater solution. Females were returned to the conditioning tank until the next spawning trial while males were removed.

Eggs were counted with a Coulter counter fitted with a standardized 400 μm aperture. Three counts were made from each spawn in one of three dilutions (1/100, 5/100, or 10/100). Fixed eggs (n = 100) for each individual spawning event (or approximately 23,000 total eggs) were measured using an ocular micrometer. A correction factor for swelling due to fixation was calculated based on samples which were measured in both a fresh and a fixed condition. Following the 10th trial, females from ARC (n = 10), ARC × SCW (n = 8), and SCW (n = 9) were sacrificed for histology. Oocyte area/follicle area measurements were made using ocular micrometer and Wiebel counting grid.

Analysis of variance was performed using a general linear model and significant differences in stocks ($P \leq 0.05$) were separated using least squared means tests (SAS 1985). Fecundity parameters tested were eggs shed per female and per spawn, number of spawns, egg size and oocyte area/follicle area. Spawning peaks during the 10 laboratory spawning trials were defined as those spawning trials with significantly greater number of females shedding eggs.

RESULTS

Field Evaluation

Sexual maturity, defined as the SL class interval at which the sex ratios did not significantly differ from 1:1 (Eversole et al. 1980), occurred in ARC and ARC × SCW at 30–35 mm SL. In SCW this occurred at 20–25 mm SL. Mass mortality of SCW was observed in June 1985, following movement back to Folly River in May. Of the 60 SCW clams collected from June through August 1985, only 21 had developed gonads and all of these appeared to be reabsorbing gonadal tissue. Sex ratio favored the female clams 9.5:1.0 and all but one female was ≥35 mm SL.

Differentiated condition varied significantly with month ($p \leq 0.01$) and interaction ($p \leq 0.05$) but not with stock. Percent of population in a differentiated state was 47% from July to November 1984, 74% in December and January 1985, and 94% from February to April 1985 (Figure 1). Mean level of differentiation was only significantly different ($p \leq 0.05$) in July 1984 when the ARC × SCW was lower than the other two stocks (Figure 1). SCW was not included in the statistical analysis after April 1985 because of the movement of clams back to Folly River in May 1985 and the low differentiation levels resulting from the apparent reabsorption of gametes. Level of differentiation from May through August 1985 of the other two stocks was not significantly different to differentiation level for the three months prior to the move (February–April 1985).

Significant differences ($p \leq 0.01$) were found among stocks, months and interaction of month and stock in level

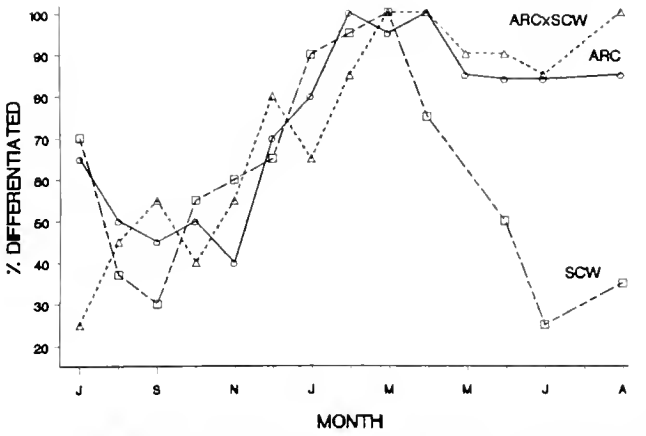

Figure 1. Mean percent level of gonad differentiation of stocks (ARC, Aquaculture Research Corporation; SCW, South Carolina wildstock and ARC × SCW cross) of hard clams grown in South Carolina waters from July 1984 to August 1985.

of spawning condition. Although the level of spawning condition varied significantly with month and stock, the interaction term holds the important biological information indicating spawning peaks. ARC stock exhibited a trimodal spawning pattern with a smaller peak in December 1984, and major peaks in August 1984 and April 1985 (Figure 2). Two spawning peaks (July and March) occurred in the SCW. Spawning pattern of ARC × SCW was somewhat intermediate of the parental stocks.

Laboratory Spawning Trials

ARC × SCW stock shed significantly ($p \leq 0.05$) more eggs than either parental stock, but no significant differences were detected between parental stocks (Table 1). SCW had a significantly ($p \leq 0.05$) greater amount of oocyte area/follicle area (follicular condition) following 10 spawning attempts than the other two stocks (Table 1). The higher oocyte area/follicle area of SCW suggests an ability to continue spawning past the 10th trial and a higher potential total fecundity. On the other hand, the relatively low oocyte area/follicle area in ARC and ARC × SCW indicate a more complete spawning or spent condition.

Mean number of spawns in SCW and ARC × SCW females was significantly (≤ 0.05) higher than the ARC stock (Table 1). The SCW was the only stock to have a female spawn in all 10 trials. The significantly ($p \leq 0.05$) lower mean number of eggs/spawn by females of SCW also indicates a more gradual release of eggs over this period, a characteristic of "dribble" spawning. The majority of SCW and ARC × SCW clams spawned three times during the 30-day period. These times, statistically significant spawning peaks, were similar in SCW and ARC × SCW with a 9–12 day recovery between spawns (Figure 3). ARC delayed most of its spawning until the last three trials, and these trials composed three of the four spawning peaks. The ARC stock had only one peak (10th) in common with other two stocks (Figure 3).

Size of fresh eggs was 90.075% of formalin fixed egg size. Egg diameters (fixed) were significantly different ($p \leq 0.05$) among stocks; however, the mean difference was only 0.74 μm. Egg size decreased significantly ($p \leq 0.05$) with spawning trial, but this decrease did not vary significantly among stocks (Figure 4). Mean egg size from spawns 1–4 ($\bar{x}$ = 83.72 μm) were significantly ($p \leq 0.05$) larger than eggs in spawns 7–10 ($\bar{x}$ = 80.60 μm).

Three hermaphrodites were discovered among 45 ARC clams selected for spawning and were not included in the statistical analysis. These hermaphrodites spawned first as females and then as males. A few oocytes were present within the follicles of these hermaphrodites after 10 spawning trials. Sperm of two hermaphrodites used to fertilize eggs successfully produced larvae. The sex ratios (f:m) were 2.4:1.0 in ARC, 1.0:1.1 ARC × SCW, and 1.4:1.0 SCW.

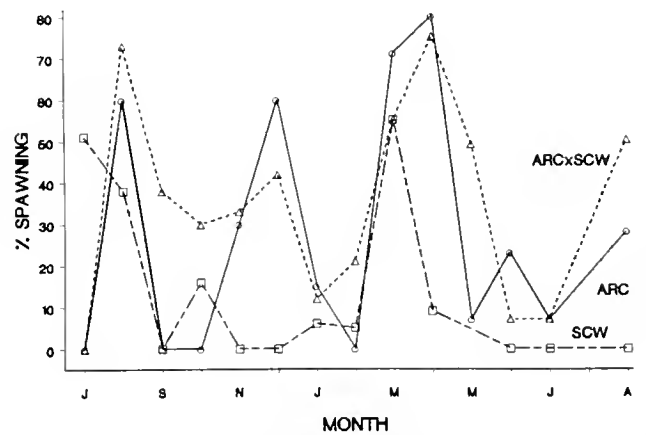

Figure 2. Mean percent level of spawning condition for stocks (ARC, Aquaculture Research Corporation; SCW, South Carolina wildstock and ARC × SCW cross) of hard clams grown in South Carolina waters from July 1984 to August 1985.

DISCUSSION

Bricelj and Malouf (1980) found the smallest female hard clam with mature ova to be 33.1 mm SL in Long Island Sound, New York. Eversole et al. (1980) found active female clams in South Carolina between 22–26 mm SL. Size at sexual maturity, when the sex ratio equalled 1:1 (Eversole et al. 1980), was smaller in the southern stock (SCW) than in the northern stock (ARC), while ARC × SCW matured at a size similar to that of ARC. Larger maturation size should be a valuable stock trait in selecting faster growing clam stock.

Spawning pattern in SCW was similar to the bimodal patterns reported for hard clams in South Carolina (Eversole et al. 1980, Manzi et al. 1985) and Georgia (Pline 1984). While the spawning pattern for the ARC stock was similar to that reported by Dalton and Menzel (1983) for a hard clam stock transplanted from Delaware to northwest Florida. Hard clams from areas near Aquaculture Research

TABLE 1.

Fecundity, egg diameters (fixed), follicular condition and spawning results for the Aquaculture Research Corporation stock (ARC), South Carolina wildstock (SCW), and the cross (ARC × SCW) of 45 clams thermally induced to spawn 10 times from January 24 to February 22, 1986.

Parameter	Stock		
	ARC	ARC × SCW	SCW
Number of females	29	21	19
SL (mm)	52–74	51–65	42–54
$\bar{x}$ eggs/female ($\times 10^5$)	13.5[a]	18.8[b]	7.73[a]
	(0.1–34.3)	(3.9–33.1)	(1.0–18.9)
$\bar{x}$ eggs/spawn ($\times 10^5$)	5.2[a]	5.1[b]	1.8[b]
	(0.1–31.5)	(0.3–15.4)	(0.1–10.2)
$\bar{x}$ egg size (μm)	80.63[a]	82.11[b]	81.32[c]
	(42–107)	(40–110)	(40–103)
$\bar{x}$ spawns/female	2.6[a]	3.7[b]	4.3[b]
	(1–5)	(1–6)	(1–10)
$\bar{x}$ oocyte area/follicle area ($\times 10^{-2}$)	23.0[a]	26.0[a]	36.2[b]
	(8–47)	(10–50)	(24–50)

Letters identify significantly different groups ($p \leq 0.05$).

Corporation in Massachusetts have a unimodal spawning pattern with a spawning peak in summer (Loosanoff 1937, Kassner and Malouf 1982). The differences in ambient conditions between Massachusetts and South Carolina as recognized by ARC clams may account for some of the variation in the spawning pattern at the two localities. However, the intermediate nature of the spawning pattern of the ARC × SCW suggests that spawning pattern has some genetic component. Dillon (personal communication, 1985) has observed electrophoretic differences among these stocks. Loosanoff (1969) indicated that there are physiologically different races of *C. virginica* based on different temperatures for maturation of the gonad and initiation of spawning. He found generally that oysters from northern areas began gametogenesis at cooler temperatures than oysters from southern areas. Loosanoff et al. (1951) also observed that a Long Island population of *Mercenaria* had a particular temperature for larval setting and growth, and further hypothesized that different bivalve populations have race-specific growth and survival temperatures.

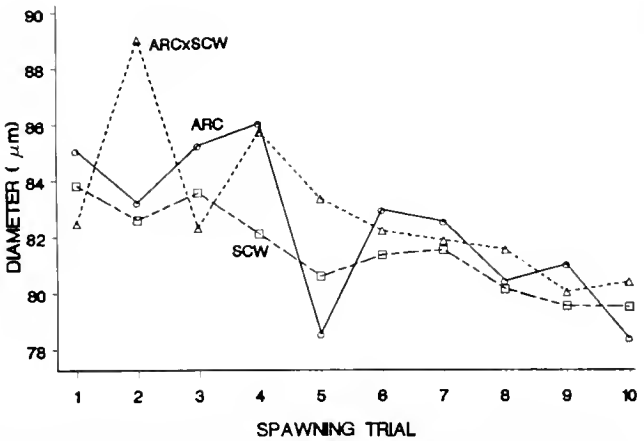

Figure 4. Mean egg diameter (μm) of stocks (ARC, Aquaculture Research Corporation; SCW, South Carolina wildstock; and ARC × SCW cross) thermally induced to spawn 10 times.

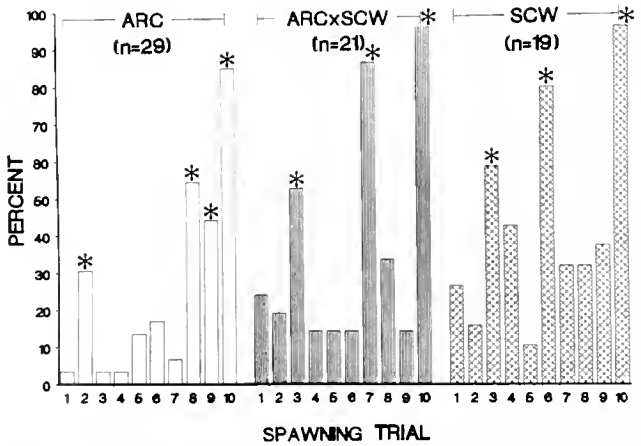

Figure 3. Percent of female hard clams of stocks (ARC, Aquaculture Research Corporation; SCW, South Carolina wildstock; and ARC × SCW cross) spawning after each of 10 thermal spawning inductions. Significant spawning peaks indicated by an asterisk.

In laboratory trials ARC appeared to require more time for conditioning than the other two stocks. It is not unreasonable to assume that clams from more northerly latitudes which begin gametogenesis at lower temperatures would require more degree-days to complete gametogenic conditioning to be able to release eggs during the more uniform warmer temperatures of summer. Lannan et al. (1980) demonstrated that the optimum window of gametogenic conditioning measured in terms of larval oyster survival varied from stock to stock, and that gametogenic rate of oysters was under stringent genetic control (Lannan 1980). Loosanoff (1969) observed stock specific temperatures for the onset of gametogenesis in oysters. Obviously, condi-

tioning temperatures need to be considered along with calendar date in establishing a stock specific conditioning protocol.

The egg size of the ARC stock conditioned and spawned in South Carolina was significantly smaller than the other two stocks. ARC stock, which typically conditions at lower temperatures than southern stocks (e.g., SCW), may have been stressed at the higher temperatures found in South Carolina and used in this experiment (19°C). Barber and Blake (1983) attributed the smaller egg size with decreasing latitudes in the bay scallop, *Argopecten irradians irradians*, to an increased metabolic demand at warmer temperatures. Thermal stress has also been shown to lower fecundity and reduce the size of eggs in the mussel, *Mytilus edulis* (Bayne et al. 1978).

Bricelj and Malouf (1980) attributed the observed decrease in the egg size as hard clams continued spawning to either rapid (incomplete) gametogenesis or an increase in ambient water temperature. While egg size decreased progressively as ARC, SCW and ARC × SCW spawned over the 10 trials, these stocks were not exposed to progressively increasing temperatures during the 30-day period. This suggests that the decrease in egg size was probably a result of the stress associated with repeated force spawnings and/or inadequate time for complete gametogenic recovery. This scenario appears exaggerated in the ARC stock which exhibited the smallest eggs and the greatest decrease in egg size during the study.

Markow (1982) observed that frequency of mating was related to gametogenesis cycles and an inherited trait among invertebrate species. We present evidence in this study to indicate that a genetic basis for spawning frequency may exist in hard clam stocks. For example, SCW and ARC × SCW had a similar number of spawns/female while the ARC was statistically different. Peak events for SCW and ARC × SCW stocks were similar, occurring 9–12 days apart, while the ARC spawned early and at the end of the spawning trials. SCW gradually released its eggs characteristic of a "dribble" spawner, while the other two stocks released the majority of their eggs in few spawning events as is the case with a mass spawner. The cross (ARC × SCW) appeared to have characteristics which resembled both the paternal parent (fecundity, conditioning and spawning pattern) and maternal parent (mass spawner).

Broodstock management is a vital step in fulfilling the potential of hard clam aquaculture. It is also apparent from these studies that geographically isolated stocks do have different conditioning and spawning patterns, as well as different responses to induced spawning cues. Careful study of stocks and methods of inheritance may provide us with the means for more rapid domestication and increased production of the hard clam. Identification of specific beneficial traits will also be useful in developing hatchery protocols and breeding programs.

ACKNOWLEDGMENTS

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FEEDING RATES IN HARD CLAM (*MERCENARIA MERCENARIA*) VELIGER LARVAE AS A FUNCTION OF ALGAL (*ISOCHRYSIS GALBANA*) CONCENTRATION

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ABSTRACT The retention efficiency (clearance efficiency) in hard clam (*Mercenaria mercenaria*) veliger larvae was measured to be maximal for algal cells with a diameter of 4 μm. Smaller particles down to 2 μm were retained with rapidly declining efficiency, and the maximum ingestable algal size of 3 days old larvae was ca. 6 μm. The rates at which three size groups of hard clam larvae cleared suspensions of maximally retained algae (*Isochrysis galbana*) were measured at different concentrations of algae. Maximum clearances (28.5°C) were recorded at about 8 algal cells μl^{-1}. A decrease in the clearance capacity was recorded below this algal concentration, and above an exponential decrease in clearance was observed. The equation for fitted curves for clearance (F, $\mu l\ h^{-1}$ $larva^{-1}$) as a function of algal concentration (C, cells μl^{-1}) was $F = aC^{-1}e^{-8/C}$, where a = 250 for larvae of 93 μm shell height and 3 days old, 540 for larvae of 136 μm and 8 days, and 1200 for larvae of 164 μm and 11 days). The ingestion rate increased sigmoidally with algal concentration to approach a plateau, and from this the minimum algal concentration resulting in maximal growth rate was predicted to be 40–60 *I. galbana* cells μl^{-1}.

KEY WORDS: *Mercenaria mercenaria*, hard clam larvae, retention efficiency, clearance, ingestion rates

INTRODUCTION

The hard clam, *Mercenaria mercenaria*, has been commercially exploited in the salt marshes along the Atlantic seaboard of North America for many years. Due to overfishing, clamming is now sporadic; but the coastal waters are believed to be suitable for commercial culturing, and mariculture of the hard clam may be one means of increasing production (Walker 1983 and 1985, Walker and Humphrey 1984). Laboratory cultivation of seed clams to be planted in the intertidal zone of the salt marshes today is being performed at an increasing number of hatcheries in the U.S.A. Hatchery-reared, clam larvae are most often fed mass-cultured *Isochrysis galbana*, and economical designs of controlled sytems for rearing clam larvae are desirable as large-scale production of algae is costly. Cultural systems that can bring clam larvae successfully to metamorphosis on a minimum ration of algae may be constructed on the basis of knowledge concerning the rate of food consumption in relation to algal concentration and growth of the larvae (Epifanio, Srna and Pruder 1975, Winter 1978). This paper describes retention efficiency and feeding rates of hard clam larvae as a function of algal concentration.

MATERIALS AND METHODS

The work was carried out at the Skidaway Institute of Oceanography, Georgia, U.S.A., during July 1987.

Veliger larvae of the hard clam, *Mercenaria mercenaria* (L.) were obtained from a cohort being reared at 28.5°C in the shellfish hatchery on an abundent diet of *Isochrysis galbana*. The larvae reached metamorphosis within 12 days.

Larvae to be used for experiments were retained on a filter with a mesh size of 30 μm, mixed in a small volume of seawater, counted, and transferred to 1800 ml glass-beakers filled with filtered (0.5 μm) seawater to make up a concentration of 11–18 larvae ml^{-1}. The larvae were starved for 3 h before the experiments. This was done to standardize the experimental conditions and to avoid possible influence on feeding rates due to filling of the gut prior to the experiments.

The volume of water cleared of particles per unit time, clearance (F, ml min^{-1}), by the veliger larvae was estimated by measuring the reduction of added algal cells to the glass-beaker with a known volume of water (V, ml) using the formula (Coughlan 1969, Riisgård et al. 1980): $F = V/t \times \ln C_O/C_t$, where t is the time in minutes C_O and C_t are the particle concentrations at time *0* and time t.

Size distribution and concentration of particles were measured by an electronic particle counter, Coulter Counter, Model TA II with a population accessory plotter and a 100 μm orifice tube. Appropriate mixing was ensured by aeration. All experiments were performed at 28.5°C and 28°/00 S.

The retention spectrum of 3 days old larvae was obtained by expressing the clearance of added particles of different size as per cent of the highest measured clearance. The particles used were: *Cryptomonas* sp. (ca. 5–9 μm), *Isochrysis galbana* (3–4 μm) and bacteria (ca. 2 μM) occuring in the algal cultures used. The algae were chosen because of their nearly spherical shape, so that the diameter measured with the Coulter Counter was reliable. The different particle sizes were simultaneously measured in channel 3 to 9 of the Coulter Counter. At the beginning of an experiment it was ensured that approximately the same number of particles were counted in channel 4–9 (4–5000 counts ml^{-1}). The number of particles in channel 3 (2.0 μm) was about 8000 ml^{-1}. The experimental time was 2 h

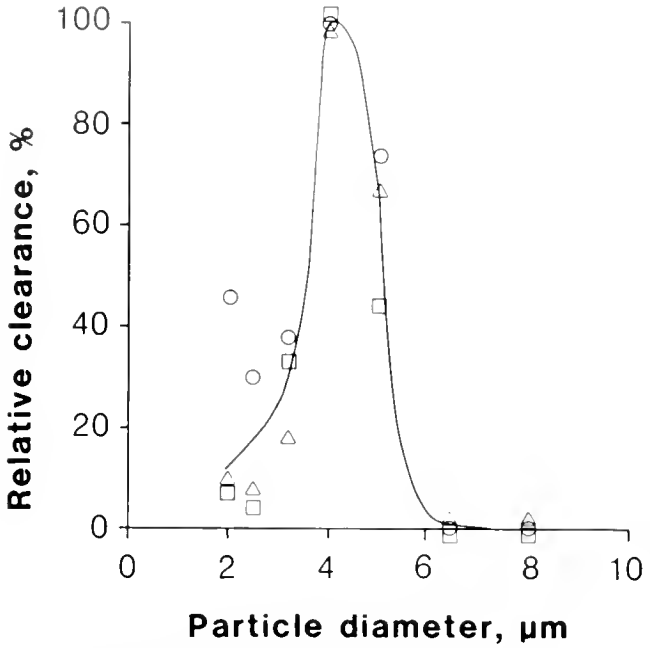

Figure 1. *Mercenaria mercenaria.* **Retention spectrum of 3 days old larvae. Data from 3 experiments; curve drawn by eye.**

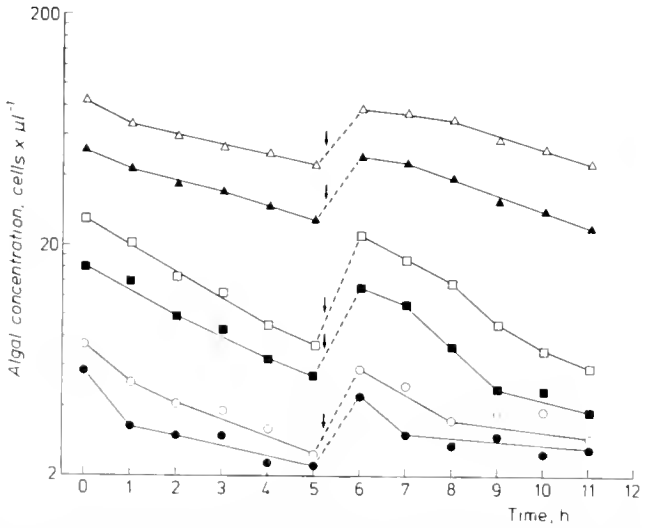

Figure 2. *Mercenaria mercenaria.* **Semi-logarithmic plot of reduction in *Isochrysis galbana* concentration due to grazing of 136 µm shell height and 8 days old clam larvae. Results from six experiments performed with the same concentration of larvae (11 larva ml^{-1}) but different initial algal concentration are shown. Arrows indicate time of algal additions. Curves are drawn by eye.**

and the maximal reduction of the fastest cleared particle size was 40–50%.

The rates at which different sized larvae cleared suspensions of *Isochrysis galbana* were measured in experiments run at different initial algal concentrations. In these experiments the concentration of the modal size range of the alga was measured as the sum of particles with mean diameters of 3.2 and 4.0 µm (i.e., channel 5 and 6 of the Coulter Counter). This was done to avoid possible interference with fecal particle production in the lower channels and to allow measurement of the clearance capacity (i.e., volume of water cleared of maximally retained particles per unit of time when the ingestion rate of the larvae is uninfluenced by filling of the gut). Samples (25 ml) for particle counting were taken every 1 h during a period of 8–11 h by means of a pipette and filtered through a 35 µm sieve to remove the larvae.

Ingestion rates were found by multiplying the clearances with the mean algal concentration at which the clearance was determined. The number of larvae ml^{-1} as well as the larval size was determined by means of an inverted microscope.

RESULTS

The retention spectrum of 3 days old veliger larvae is shown on Figure 1. There was a pronounced clearance peak for 4 µm particles. Below 4 µm the relative clearance decreased to ca. 10–30% for 2–3 µm particles, and above 4 µm there was a decrease to ca. 60% for 5 µm and then a rapid drop to zero for 6 µm and larger particles.

Figure 2 shows the reduction in algal cell concentration as a function of time in six experiments performed on hard clam larvae at different initial algal concentrations. It is seen that the reduction rate was correlated with the algal concentration. At the higher concentrations the reduction rates were lower than at intermediate concentrations. When the algal concentration droped below 3–6 cells µl^{-1} a decrease in the grazing rate was seen.

The data shown in Figure 3 were obtained by estimating the clearances for all 1-h intervals in Figure 2. Figure 3 also shows the results of similar experiments conducted with two other size groups of larvae. The mean clearance values as a function of the mean algal concentration were calculated for each concentration interval of 4 cells µl^{-1}. The fitted curves show an exponential decrease in clearance as a function of algal concentration above ca. 8 cells µl^{-1}. Below this algal concentration at which the clearance capacity was recorded, there was a decrease in clearance.

The ingestion rate as a function of algal concentration in two size groups of larvae is shown in Figure 4. The ingestion rate increased sigmoidally with food concentration and approached a plateau of 250 and 540 cells h^{-1} for 93 µm and 136 µm larvae, respectively.

DISCUSSION

Particle retention spectra of bivalve larvae have previously been recorded in mussel larvae (Riisgård et al. 1980, Sprung 1984b) and oyster larvae (Walne 1965). The retention efficiency (or "clearance efficiency") in these studies was found to be maximal for 3–4 µm particles. Smaller particles down to 1 µm were retained with de-

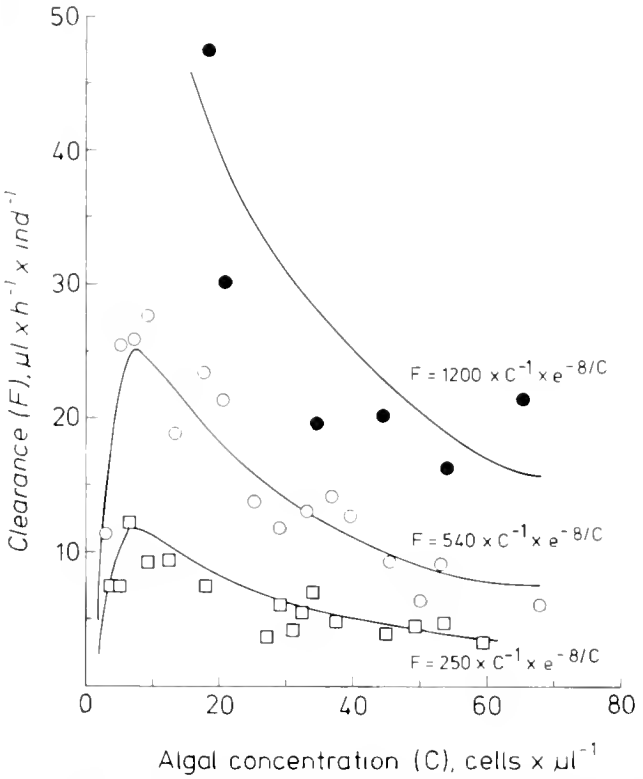

Figure 3. ***Mercenaria mercenaria.*** **Clearance as a function of algal concentration (*Isochrysis galbana*) in hard clam larvae of different size. Squares: 3 days old larvae and 93 µm shell height; open circles: 8 days old and 136 µm; closed circles: 11 days old and 164 µm. Equations for fitted curves are shown. Each point represents the mean of 3-16 measurements.**

clining efficiency and the maximum ingestable size was about 8–9 µm. The retention spectrum found in this work (Figure 1) agrees with these earlier recordnings, except that the maximum ingestable particle size was only about 6 µm.

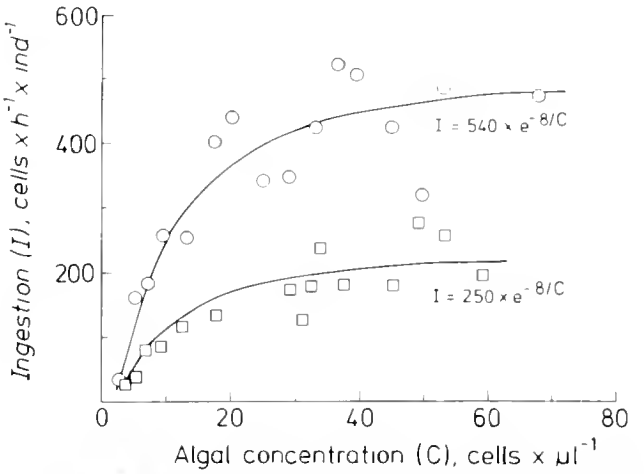

Figure 4. ***Mercenaria mercenaria.*** **Ingestion rate as a function of algal concentration (*Isochrysis galbana*) in two size groups of clam larvae. Equations for fitted lines are shown. Square: 3 days old and 93 µm shell height larvae; circle: 8 days old and 136 µm.**

Other similar unpublished studies on hard clam larvae carried out at the Environmental System Laboratory, Woods Hole, U.S.A., in November 1987 showed that the maximum ingestable particle size increased with size (age) of the larvae. Thus, 4 days old larvae did not graze on 8–10 µm algal cells while 12 days old larvae retained these particles with about 50% efficiency. The diameter of the esophagus may thus determine the upper size of algae eaten. Gallager (1988) reported that hard clam larvae continuously produce fecal pellets of about 0.2 to 1.5 µm in diameter and claimed that "this could lead to gross underestimation of clearance in the small size range". A possible influence of fecal pellets on the retention efficiency of the smaller particles in the present work can not be excluded, but as the lower particle size measured was 2.0 µm the influence of fecal pellet production seems to have been negligible.

The relationship between clearance and algal concentration has been studied in *Mytilus edulis* veliger larvae by Jespersen and Olsen (1982) and by Sprung (1984b). It was found that clearance decreased with increasing algal concentration at densities above ca. 8–10 cells μl^{-1}. Sprung also recorded declining clearances at algal concentrations below ca. 8 cells μl^{-1}. The latter phenomenon Sprung interpreted as an experimental artifact. However, the reduced slopes at the lower algal concentrations in Figure 2 indicate that in hard clam larvae the clearance does decrease at algal concentrations below 4–8 *Isochrysis galbana* cells μl^{-1}. The curves shown in Figure 3 are therefore believed to peak at about 8 cells μl^{-1}, to decrease at both higher and lower concentrations. A similar relationship between clearance and algal concentration has been observed in several marine copepods, e.g. *Acartia tonsa* (Kiørboe et al. 1985) and *Eucalanus elongatus* (Price and Paffenhöfer 1986). The reduction in clearance of *E. elongatus* was related to a reduction of the percentage of time the copepod created a feeding current. This was interpreted as an adaptation to conserve energy at low food concentrations. It remains to be verified if a similar feeding behavior exists in bivalve veliger larvae.

The maximal clearance values estimated from the equations for the fittet curves in Figure 3 for three size groups of clam larvae at 28.5°C are: 11.5, 24.8 and 55.2 $\mu l\ h^{-1}$, respectively. These values are close to and not higher than the clearance capacities measured in *Mytilus edulis* veliger larvae at 15°C (Riisgård et al. 1980, 1981). Hard clam larvae adapted to high temperatures thus seem to maintain about the same clearance rates as mussel larvae adapted to relatively low temperatures. Such a temperature adaptation has recently been found in adult bivalves (Riisgård 1988).

The decrease in clearance of mussel larvae at the higher algal concentrations was interpreted by Riisgård et al. (1980) and Sprung (1984b) as reflecting a declining clearance capacity correlated with the filling of the gut and the

digestive capacity. Recent observations made by Gallager (1988) seem partly to support this interpretation though there may be some problems with the used methodology. By using high speed video microscopy recording and subsequent counting of the number of *Isochrysis* cells transported to the mouth of tethered *Mercenaria mercenaria* larvae Gallager calculated the "filtration rate" defined as the volume swept clear per unit time (i.e. "clearance" in the present study). Gallager found that the "filtration rate" at 22°C remained constant when the cell concentration increased from 1 to 100 cells μl^{-1} (about 16 and 90 μl h^{-1} larva $^{-1}$ for 2 and 10 days old individuals, respectively), but fell to low values when the concentration was rised to 1000 cells μl^{-1}. Further, a decline in clearance below 1 cell μl^{-1} was observed.

Jespersen and Olsen (1982) found that ingestion rates and growth rates in *Mytilus edulis* larvae both reached maximum levels at *Isochrysis galbana* concentrations of 40–50 cells μl^{-1}. Sprung (1984a) recorded that the growth rate increased rapidly with the concentration of *I. galbana* up to about 10 cells μl^{-1} and that the maximum growth rate was obtained at algal concentrations between 20–40 cells μl^{-1}. The plateau of the ingestion curves shown in Figure 4 indicates that in hard clam larvae the minimum concentration resulting in maximal growth rate may be found at 40–60 *I. galbana* cells μl^{-1}. Growth of *Mercenaria mercenaria* larvae in cultures receiving 25, 50, 100, 200 and 400 *I. galbana* cells μl^{-1} has been studied by Davis and Guillard (1957). At 25 cells μl^{-1} the growth was less than at 50 cells μl^{-1}, but there was only little difference in growth rates of clam larvae over the range 50–400 cells μl^{-1}. The predicted range of algal concentration resulting in maximal growth rate is in accordance with these measurements.

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NUTRITIONAL VALUE OF MICROALGAE CULTURED IN THE ABSENCE OF VITAMINS FOR GROWTH OF JUVENILE OYSTERS, *CRASSOSTREA VIRGINICA*

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ABSTRACT Axenic strains of four algal species cultured with no supplementary vitamins in an enriched seawater growth medium (ENV) or in enriched medium also containing B_{12} and thiamine (E) were compared in terms of population growth, biochemical composition, and nutritional value to juvenile oysters, *Crassostrea virginica* Gmelin. Population growth of the pennate diatom *Nitzschia sp.* (Milford, CT isolate) and the flagellates *Pyramimonas grossii* Parke and *Dunaliella tertiolecta* Butcher was similar in a medium with (E) and without (ENV) vitamin enrichment. In contrast, the flagellate *Tetraselmis maculata* Butcher demonstrated a slower growth rate and reduced final cell concentration in ENV as compared with cultures grown in E medium Algal chemical composition in terms of protein, carbohydrate, and lipid was calculated for daily oyster feeding rations that were equalized as 0.6 ml packed cells for each group of 50 oysters. Composition of daily rations varied considerably for the three flagellates depending upon growth medium, and also varied between species. For three algal species, *Nitzschia sp.*, *P. grossii*, and *D. tertiolecta*, 12-week growth of oysters was more rapid or not significantly different when fed unialgal diets of strains cultured in E medium as compared with ENV strains. *T. maculata* cultured in the absence of vitamins contained more lipid and supported more rapid oyster growth than the control E medium culture; however, the lower stationary-phase cell yield of this alga in ENV renders the nutritional improvement of questionable practical benefit. These results demonstrate that for molluscan rearing it is not prudent to eliminate vitamin enrichments from the growth medium of algae because lower cell yields or altered biochemical composition can render no-vitamin cultures of reduced nutritional value to mollusks.

KEY WORDS: Algal culture, vitamins, juvenile oysters, nutrition, chemical composition

INTRODUCTION

In the early days of the isolation and culture of marine microalgae, only mineral solutions were used as enrichments in seawater for the culture medium because of the assumption that all aglae were autotrophs and could synthesize essential growth factors with sunlight as the energy source. It was only with the introduction of soil extract and other organic enrichments (Pringsheim 1926, 1946) that auxotrophs (species with requirements for supplementary vitamins) were isolated. Differences in vitamin requirements of algal species are not correlated with any particular ecological niche or taxonomic position (Provasoli and Carlucci 1974), and variability of vitamin requirements in different isolates of the same species has been observed (Lewin and Lewin 1960).

The requirements for vitamins in marine algae appear to be restricted to three: thiamine, B_{12}, and, less often, biotin; either singly or in combination. The incidence of auxotrophy in the green algae of the class Chlorophyceae is low, although one green alga, from the Euglenophyceae, *Euglena gracilis* var *bacillaris*, is very sensitive to B_{12} deficiency and has been used as an assay organism (Hutner et al. 1949, 1956).

Most molluscan rearing methods, either for experimental or commercial purposes, require the culture of unicellular algae as food. Different algal species are needed as food sources for larval or juvenile and adult stages of the life cycle, and a mixture of several algal species often yields more rapid growth than a single species diet (Ukeles 1975). At the Milford Laboratory of the National Marine Fisheries Service, as well as in most other institutions, different algae are cultured in a standardized medium of enriched seawater (except for the addition of silicate for diatoms). This procedure is efficient in that it avoids the time-consuming preparation of different formulations.

The commercial rearing of mollusks requires considerable volumes of algae, constituting a considerable expense, accounted for partially by the cost of seawater enrichments included in the growth medium and, partially, by time required to prepare reagent solutions. A benefit would be affected if some species could be cultured in a simpler medium without added vitamins B_{12} and thiamine.

The present report describes an investigation into the growth of several axenic algal species in two culture media, one containing B_{12} and thiamine and the other lacking supplementary vitamins. The utilization of these algae for nutrition by juvenile oysters, *Crassostrea virginica* was examined.

MATERIALS AND METHODS

Algae used in these experiments were as follows: *Dunaliella tertiolecta* Butcher, *Pyramimonas grossii*, Parke, *Tetraselmis maculata* Butcher, *Nitzschia sp.*, and as vitamin bioassay controls, *Pavlova* (*Monochrysis* Droop) *lutheri* Green, *Isochrysis galbana* Parke, and *Pavlova gyrans* Butcher. All of the algae were obtained from axenic strains

(confirmed by fluorescence microscopy with acridine orange) in the Milford Laboratory culture collection.

Initial growth experiments were conducted in an artificial seawater medium, ASP_2 (Provasoli et al. 1957), from which the complement of nine vitamins (thiamine, nicotinic acid, thymine, calcium pantothenate, para-amino benzoic acid, folic acid, B_{12}, biotin and inositol) was omitted. The water used to prepare this medium was double-distilled in two all-glass distillation units and treated with activated charcoal to remove organic residues according to the following procedure: two gms of charcoal were added to one liter of double-distilled water, mixed in a flask with a magnetic stirrer for 2 hrs, allowed to settle for 2 hrs., decanted, prefiltered on Whatman No. 1 filters, and then filtered through a series of seven Millipore* filters ranging from 8 μM to 0.2 μM. The above-mentioned algal strains have been routinely subcultured as stock cultures in the no-vitamin artificial seawater bi-monthly for the past 10 years.

For the purpose of this study, strains were transferred from no-vitamin ASP_2 into an enriched natural seawater medium, ENV, prepared as per E medium (Ukeles 1973) but with vitamins eliminated. E medium is routinely used at the Milford Laboratory for the semi-continuous mass culture of algae for feeding larval, juvenile, and adult mollusks. The formulation of one liter of ENV medium is as follows: seawater, 500 ml; KH_2PO_4, 20 mg; $NaNO_3$, 300 mg; NaFe Sequestrene (Geigy), 5 mg; Tris(hydroxymethyl)aminomethane, 1.0 gm; $CuSO_4 \cdot 5H_2O$, 9.8 ng; $ZnSO_4 \cdot 7H_2O$, 22 ng; $CoCl_2 \cdot 6H_2O$, 13 ng; $MnCl_2 \cdot 4H_2O$, 180 ng; $Na_2MoO_4 \cdot 2H_2O$, 6.3 ng; pH adjusted to 8.0, and brought to final volume with glass-double-distilled H_2O (E medium is identical but with added thiamine HCl, 0.3 mg/l, and B_{12}, 3 μg/l). Seawater used in the medium was filtered through 1-μm polypropylene and 0.5-μm glass-fiber cartridges and passed through an Aquafine (Model PVCL-1) ultra-violet sterilizer unit. Both seawater and distilled water in the experimental medium were treated with activated charcoal as described above.

All media were dispensed as 10 ml aliquots into 20 × 150-mm Pyrex screw-capped test tubes. The use of cotton plugs was avoided throughout these experiments because cotton contains a high vitamin component (Robbins and Schmitt 1945). Liners and adhesive residues in test tube caps were removed because toxins can be released from the cap liners (personal observation, Ravenna Ukeles). Test tubes were brushed by hand with a mild detergent, rinsed, and again washed in a Heinicke dishwasher, followed by three one-hour immersions in boiling distilled water. Tubes were then heated in an oven at 200°C to inactivate residual organic compounds.

After 1 year of bi-monthly subculture in the ENV medium, daily growth measurements were taken of species cultured in the enriched seawater medium with and without vitamins. Steam-sterilized test tubes containing 10 ml media were inoculated with stock cultures from the early stationary phase; inoculum volume was adjusted to yield an initial population of 2×10^5 cells/ml. Cultures were incubated in a GPI incubator (Model RI) at 20°C with a 12 hr light/dark cycle providing illumination of about 450 $\mu Em^{-2}s^{-1}$.

Density of growth was determined by reading % transmittance of triplicate cultures in a Bausch & Lomb Spectronic 20 at 520 nm. New culture test tubes were used in these experiments and selected for size and equivalency of transmittance so that they could serve as cuvettes. This procedure made it possible to determine changes in density of algae in the same culture tube over a period of 28 days.

Cultures were increased in volume through a series of increasingly larger Erlenmeyer flasks to a final volume of 1500 ml in Fernbach flasks to provide inocula for 20-liter carboy culture assemblies (Ukeles 1973). Axenic carboy cultures were operated semi-continuously, i.e., 6 l of sterilized medium were added to each culture (18 l total volume) once a week to replace volumes harvested. Aliquots of algal suspension for feeding oysters were harvested each weekday morning. There was little change in culture density from Monday through Friday, indicating that cultures were in the stationary phase of the growth cycle throughout harvest.

Analyses of algal chemical constituents were conducted according to the methods described by Wikfors et al. (1984). The basic procedures were taken from the following sources: for protein, modified from Dorsey et al. (1977, 1978); for carbohydrate, Kochert (1978); for total lipid, Mukerjee (1956) as adapted by Strickland and Parsons (1977). Semi-continuous carboy cultures were sampled for analyses five days after the addition of 6 liters of sterile medium.

Feeding experiments with laboratory-reared juvenile oysters, *Crassostrea virginica*, were conducted in chambers especially designed for this purpose (Ukeles and Wikfors 1982). Fifty weighed oysters were placed in each chamber screen (each group of 50 was of equivalent weight) where they were constantly washed by flowing seawater. Filtration of seawater to 0.5 μm was accomplished by a series of polypropylene and glass fiber cartridges, followed by treatment with an ultraviolet sterilizer and an activated carbon cartridge. The flow of seawater was temporarily stopped each day at the same time for 4 hours during which time algal food sources were introduced to the chambers. The daily algal ration for each group of 50 oysters was 0.6 ml packed cells as determined by centrifugation (975 g for 5 min) in modified Hopkins tubes (Ukeles 1973). Feeding the same packed cell volume of algae provided each group of oysters with the same cytoplasmic volume for all algal diets.

*Use of trade names does not imply endorsement by the National Marine Fisheries Service.

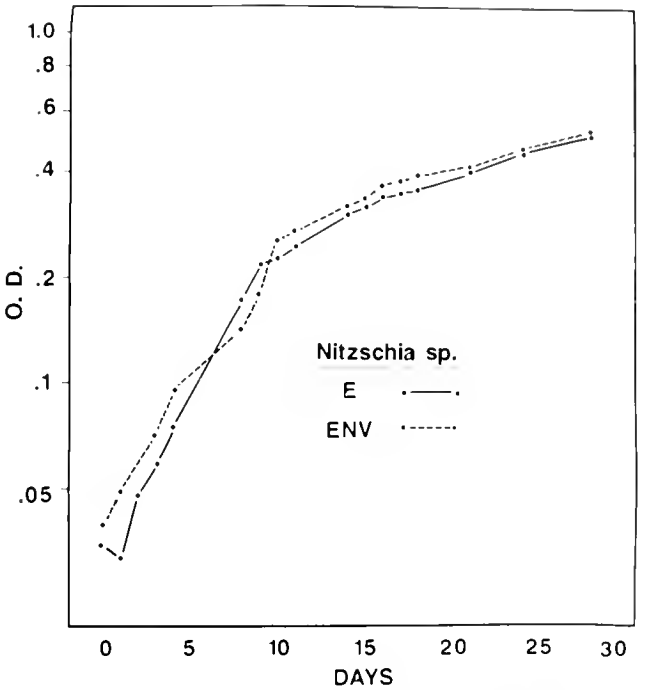

Figure 1. Growth of *Nitzschia sp.* in enriched seawater growth medium with added vitamins B_{12} and thiamine (E) or within vitamin enrichment (ENV).

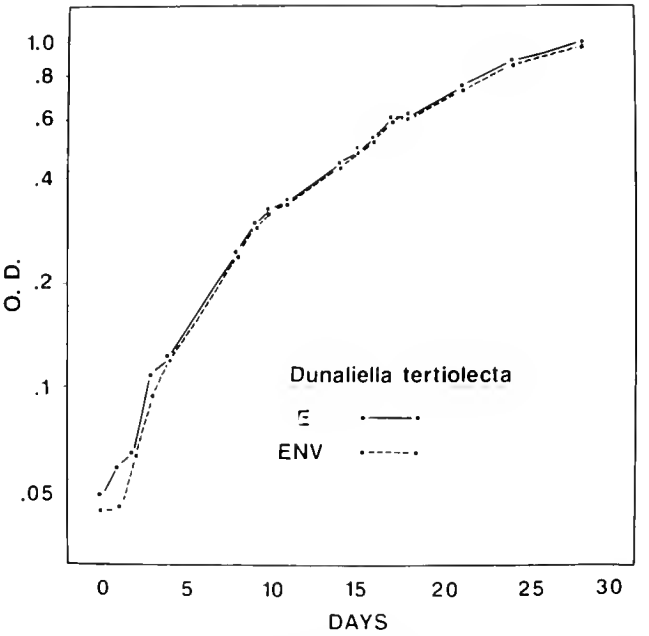

Figure 2. Growth of *Dunaliella tertiolecta* in enriched seawater growth medium with added vitamins B_{12} and thiamine (E) or without vitamin enrichment (ENV).

Chambers were dismantled each week and cleaned; oysters were weighed and observed for viability. After this procedure, living oysters were replaced on the screen and chambers were reassembled. The experiment was continued for twelve weeks.

RESULTS

Growth of *P. lutheri*, *I. galbana*, and *P. gyrans*, which all require vitamins (Provasoli and Carlucci 1974), ceased in the third subculture in the artifical seawater medium without vitamins. This observation provided evidence that the medium was, indeed, deficient in vitamins B_{12} and thiamine. A similar bioassay was conducted to ensure that the enriched seawater without vitamins did not contain sufficient amounts of B_{12} and thiamine to support growth of the auxotrophs *P. lutheri* and *I. galbana*.

Of the four algal species studied, three, *Nitzschia sp.*, *D. tertiolecta*, and *P. grossii*, demonstrated nearly identical growth in the presence or absence of vitamins (Figures 1–3, standard deviations were less than 10% of mean culture densities). *T. maculata* showed considerable decreases in growth rate and maximal population in the medium without vitamins as compared with E medium containing vitamin enrichments (Figure 4). Successful scale-up to semi-continuous carboy assemblies confirmed that these algae could be cultured reliably in large volumes without vitamin enrichment.

Analyses of these algal strains for gross chemical composition revealed potential differences in nutritional value for juvenile oysters. The composition of *Nitzschia sp.* was similar in media with and without vitamins, except for carbohydrate which was significantly different between strains (Table 1), and growth of oysters fed the two strains was statistically (ANOVA, $p = 0.5$) identical (Figure 5). In contrast, the other three algal species showed large and sig-

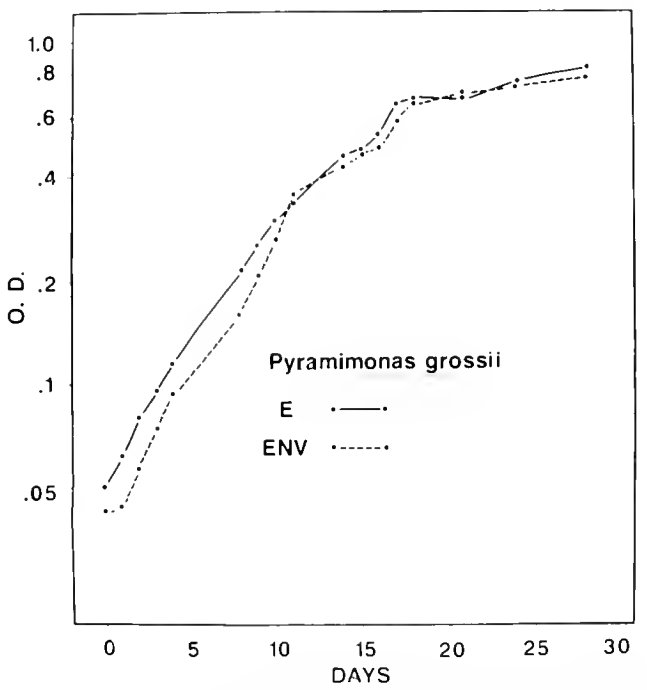

Figure 3. Growth of *Pyramimonas grossii* in enriched seawater growth medium with added vitamins B_{12} and thiamine (E) or without vitamin enrichment (ENV).

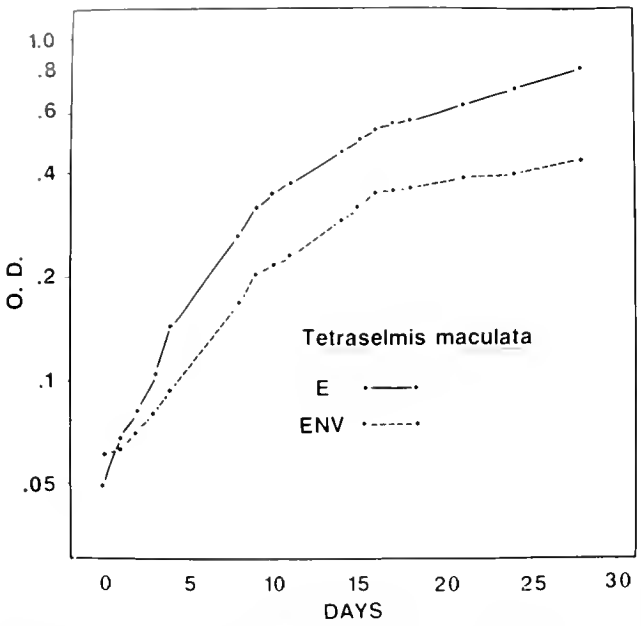

Figure 4. Growth of *Tetraselmis maculata* in enriched seawater growth medium with added vitamins B_{12} and thiamine (E) or without vitamin enrichment (ENV).

nificant (ANOVA, p = 0.05) differences in gross chemical composition when cultured in the two media. *D. tertiolecta* cultured in the absence of vitamins accumulated less carbohydrate, but more protein, than cells grown with vitamin enrichment (Table 1). Oysters fed either *D. tertiolecta* strain grew at statistically (p = 0.05) identical rates (Figure 6). *P. grossii* cultured in the absence of vitamins was a considerably poorer oyster diet than *P. grossii* cultured with vitamin enrichment (Figure 7), this observation correlating with higher contents of all components measured in the latter cells (Table 1). Only *T. maculata* cells cultured without vitamins were of greater nutritional value to oysters than control E medium cultures (Figure 8). In this case, *T. maculata* grown without vitamins contained significantly more lipid and protein, but less carbohydrate, than the same species cultured with supplemental vitamins (Table 1).

DISCUSSION

The need to economize the expense of algal culture for rearing invertebrates in the laboratory and commercial hatchery has been identified as having high priority (Ukeles 1971, Persoone and Claus 1980, Enright et al. 1986a). Based upon algal growth data alone, one could be misled into concluding that a benefit would be accomplished simply by using a vitamin-free medium to culture large volumes of autotrophic algal species for molluscan food sources. For three algal species tested in the experiments reported here, rates of growth and maximal populations were identical in media with and without the vitamins B_{12} and thiamine. A reduction in growth rate and maximal population of *T. maculata* cultured without vitamins was demonstrated.

Although algal growth characteristics were similar in the two media, it is curious that the absence of vitamins affected metabolism somewhat differently in each of the flagellates. *D. tertiolecta* protein is higher in ENV, but the storage produce carbohydrate is increased in E medium. In *P. grossii*, dry weight, protein, carbohydrate and lipid are all higher in cells from E than from ENV medium. Analyses of *T. maculata* yielded considerably higher lipid values in both culture media, as compared with other algal species; furthermore, *T. maculata* rations from ENV contained more lipid, but less carbohydrate, than cells from E medium.

Differences in chemical composition of the algal diet have been shown to influence nutrition of larval and juvenile oysters (Webb and Chu 1983, Wikfors et al. 1984). Numerous reports have focused upon the importance of lipids in molluscan nutrition. Millar and Scott (1967) showed that lipid was the major energy reserve of *O. edulis* larvae during starvation, and growth rates of newly-released *O. edulis* larvae were shown to correlate with lipid content (Helm et al. 1973). Holland and Spencer (1973) also concluded that lipid was the major energy source of larvae and young spat of *O. edulis*. The importance of carbohydrate in the diet of *C. virginica* juveniles has also been

TABLE 1.

Characteristics of 0.6 ml packed-cell volumes for eight algal diets fed daily to oyster populations in each chamber [mean of 4 replicates (sd)].

Species	Growth Medium	Cell Number × 10^9	Dry Weight mg	Protein mg	Carbohydrate mg	Lipid mg
Nitzschia sp.	E	2.9 (0.24)	72.3 (2.02)	33.4 (2.26)	10.4 (0.29)	1.58 (0.09)
	ENV	3.1 (0.08)	80.5 (0.99)	34.5 (0.52)	*8.35 (0.36)	1.54 (0.08)
D. tertiolecta	E	1.4 (0.40)	113 (16.9)	44.4 (5.06	35.1 (0.90)	2.22 (0.07)
	ENV	1.5 (0.43)	131 (19.3)	*85.3 (3.41)	20.7 (0.32)	1.98 (0.07)
P. grossii	E	2.4 (0.31)	200 (14.3)	111 (6.71)	29.5 (0.45)	3.67 (0.13)
	ENV	*1.8 (0.27)	*92.7 (17.9)	*63.6 (1.69)	*27.9 (1.29)	*2.36 (0.05)
T. maculata	E	1.9 (0.09)	215 (15.9)	66.8 (2.85)	51.4 (0.97)	18.0 (0.34)
	ENV	1.9 (0.17)	218 (13.7)	*75.4 (3.17)	*22.0 (0.79)	*24.2 (0.45)

* Means significantly different (ANOVA p = 0.05, Duncan's multiple range test)

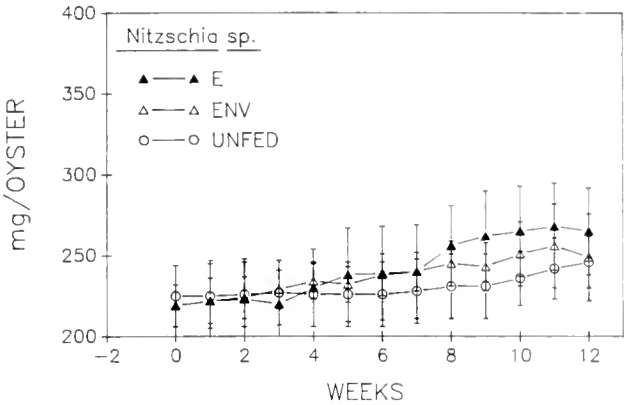

Figure 5. Growth of oysters fed a unialgal diet of *Nitzschia sp.* that was cultured in seawater growth medium with added vitamins B_{12} and thiamine, E, or without vitamin enrichment, ENV (mean live weights with standard deviations).

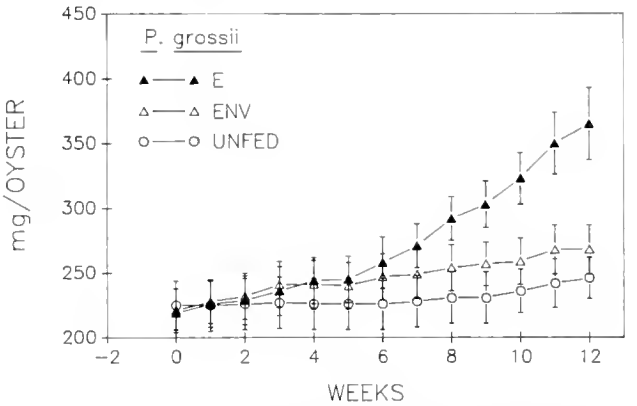

Figure 7. Growth of oysters fed a unialgal diet of *Pyramimonas grossii* that was cultured in seawater growth medium with added B_{12} and thiamine, E, or without vitamin enrichment, ENV (mean live weights with standard deviations).

reported; (Castell and Trider 1974, Wikfors et al. 1984, Enright et al. 1986a). In the present study, the smaller amounts of the storage products carbohydrate and lipid in *Nitzschia sp.* and ENV-cultured *P. grossii,* as compared with flagellate cultures from E medium, and the effects of these algae on oyster growth, support the contention that these dietary constituents are important. *Nitzschia sp.* was a poor food source (not significantly different than unfed controls), regardless of culture medium, and daily oyster rations of this diatom contained the lowest concentrations of both lipid and carbohydrate. The observation of poor oyster growth on unialgal diets of *Nitzschia sp.* is similar to results obtained by feeding *C. virginica* juveniles the morphologically-similar diatom, *Phaeodactylum tricornutum* (Epifanio and Mootz 1975, Epifanio et al. 1976, Ukeles and Wikfors 1982).

The relative nutritional values of E and ENV strains of the chlorophyte flagellate *D. tertiolecta* for juvenile oysters suggests that differences in protein and carbohydrate between these strains are not sufficient to affect oyster growth.

The relative ranking of *P. grossii* diets in the present study was dependent upon the growth medium: *P. grossii* E supported statistically greater oyster growth than *P. grossii* ENV, which was statistically identical to the unfed control; this difference evidently related to the much higher contents of all nutritional components in daily feeding rations of E vs. ENV cultures. Species of *Pyramimonas* have received little attention as molluscan foods. Walne (1970) reported that *P. grossii* appeared to be a "reasonably good" food for juvenile clams, *Mercenaria mercenaria,* but he was not able to complete experiments because of problems in culturing this alga. Dupuy et al. (1977) reported that a mixed diet including *Pyramimonas virginica* (nom. prov.), provided "more than adequate nutrition" for larval oysters, *C. virginica.* The present report demonstrates that a unialgal diet of *Pyramimonas grossii* cultured in E medium

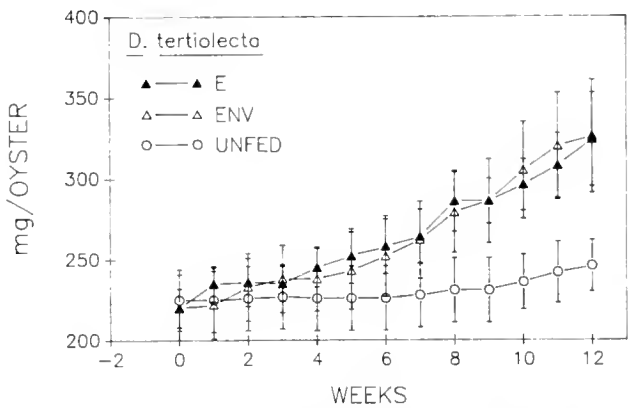

Figure 6. Growth of oysters fed a unialgal diet of *Dunaliella tertiolecta* that was cultured in seawater growth medium with added B_{12} and thiamine, E, or without vitamin enrichment, ENV (mean live weights with standard deviations).

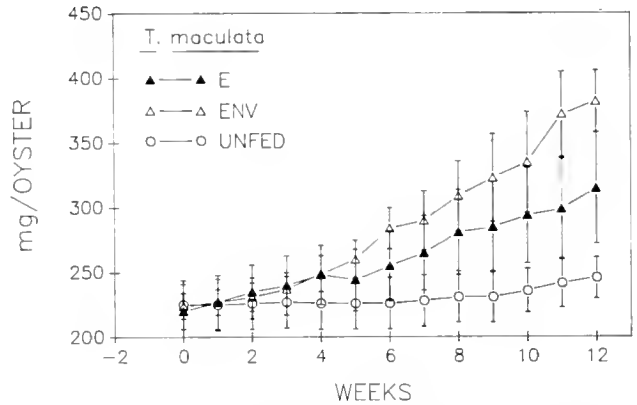

Figure 8. Growth of oysters fed a unialgal diet of *Tetraselmis maculata* that was cultured in seawater growth medium with added B_{12} and thiamine, E, or without vitamin enrichment, ENV (mean live weights with standard deviations).

with vitamin enrichment supports very rapid growth of oysters, but that this alga cultured without vitamins is a poor oyster food source.

Reasons for differences in growth of oysters fed *P. grossii* and *T. maculata* cultured in the two media are not completely clear, but can possibly be accounted for by differences in both total lipid and component fatty acids. The importance of the long-chain polyunsaturated fatty acids, particularly 20:5w3 and 22:6w3, in nutrition of marine animals was first reported by Kanazawa et al. (1979), who noted that even though marine animals in general are metabolically capable of synthesizing these fatty acids from the precursor, linolenic acid, they cannot produce enough to meet physiological needs. This "functional" requirement has been reported in several studies of juvenile oysters, *Ostrea edulis* (Langdon and Waldock 1981, Enright et al. 1986a, b). These studies noted that oyster growth was best when both 20:5w3 and 22:6w3 fatty acids were included in the alal diet; however, Langdon and Waldock (1981) observed that either fatty acid alone would partially satisfy the dietary requirement. Evidence in the literature suggests that *Pyramimonas* contains a higher percentage of 22-carbon fatty acids that *Tetraselmis*. Holz (1981) reported that 22-carbon fatty acids account for 13–14% of the total hydrogenated fatty acid methyl esters in two strains of *Pyramimonas sp.*, as opposed to only traces in *T. apiculata* and *T. gracilis*. The *Tetraselmis* species analyzed in the same study contained a higher percentage of 20-carbon fatty acids than the *Pyramimonas* strains, but *Pyramimonas* did contain some 20-carbon fatty acids. It is possible, therefore, that the *T. maculata* diets in the present study were deficient in 22:6w3 fatty acid as compared with *P. grossii* cultured in the presence of vitamins. Langdon and Waldock (1981) considered *T. suecica* to be deficient in 22:6w3 for *C. gigas* nutrition, even though this was compensated for somewhat by a relatively high concentration of 20:5w3. In the present study, *P. grossii* total lipid was lower when cultured in the absence of vitamins, which suggests that this diet may have been deficient in 20:5w3 for meeting the nutritional requirements of rapidly-growing juvenile *C. virginica*. However, the possibility remains that some other aspect of algal composition or vitamin nutrition accounted for the difference in growth of oysters fed *P. grossii* or *T. maculata* cultured in the two media.

In summary, there is a clear relationship between chemical composition of algal food cultures and growth of juvenile oysters. The present study has demonstrated that the elimination of vitamin enrichments from at least one algal species, *P. grossii*, autotrophic for the vitamins B_{12} and thiamine, is not prudent because resultant changes in chemical composition reduce the nutritional quality of the algae for oysters, as demonstrated by reduced oyster growth. Cells of *T. maculata* cultured in the absence of vitamins supported more rapid growth of oysters than *T. maculata* cultured with vitamins, but this benefit is counterbalanced by a reduced cell yield in the absence of vitamins. Subtle relationships exist between algal growth media, cell yield and composition, and growth of oysters reared on cultured algae, and these must be considered when altering nutrient enrichments in media for culturing algae.

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A BIBLIOGRAPHY OF LITERATURE ON THE MANGROVE OYSTER *CRASSOSTREA RHIZOPHORAE* (GUILDING, 1828)

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ABSTRACT A total of 166 references on the biology and cultivation of *Crassostrea rhizophorae* (Guilding) are presented. Although the list is unlikely to be complete, it is the first bibliography dedicated to this species of mangrove oyster.

KEY WORDS: bibliography, *Crassostrea rhizophorae*

INTRODUCTION

The mangrove oyster *Crassostrea rhizophorae* (Guilding), a close relative of the American oyster *Crassostrea virginica* (Gmelin), is distributed between Florida and Brazil and throughout the Caribbean region. Its fast growth and delicate flavour combined with the depletion of natural stocks and the destruction of its natural habitat have made it an ideal candidate for aquaculture. However, in spite of the large number of studies addressing the biology and cultivation of this species, relevant aquaculture technology remains varied and largely in its infancy. It is felt that major factors contributing to the slow development of the industry stems from poor communication between interested groups as a result of differences in language, geographic isolation and the paucity of regional venues, be they journals or workshops, for the dissemination of information.

With the aim of surmounting some of these barriers the following bibliography has been collated. By virtue of the very problems mentioned, the list cannot be exhaustive. Nonetheless it is a starting point. It is urged that any readers aware of other pertinent literature make it available to the author or a body such as the International Development Research Centre, Canada, or the Caribbean Aquaculture Association so that in the future a complete bibliography may be published and distributed.

For bibliographic treatments of other oyster literature, including some on *C. rhizophorae* listed below, refer to Joyce (1972) and Breisch and Kennedy (1980).

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SEX RATIO, CONDITION AND GLYCOGEN CONTENT OF RAFT CULTIVATED MANGROVE OYSTERS *CRASSOSTREA RHIZOPHORAE*

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ABSTRACT Raft cultivated *Crassostrea rhizophorae* in four size classes from 20 mm to greater than 50 mm in shell height were collected monthly from May 1986 to September 1987. Oysters were sexed, condition index was determined and samples were analysed for glycogen content. Sex-ratio (proportion of males/proportion of females) varied between 0.19 and 0.59, indicating a predominance of females, and was generally high during the rainy seasons. Larger oysters tended to be female. Mean glycogen content varied between 0.13–23.86 mg · g^{-1} dry meat weight, but did not vary significantly with either shell height or sex. An apparent cyclicity in condition index was not reflected in glycogen content but was related to periods of post-spawning occurring towards the end of each rainy season.

KEY WORDS: *Crassostrea rhizophorae*, sex, glycogen, condition, raft cultivation

INTRODUCTION

Mangrove oysters, *Crassostrea rhizophorae* (Guilding) have been cultivated in Jamaica since 1977 employing a low-technology, 'off-bottom', hanging method (Wade et al. 1981). Intertidally collected spat are held subtidally from bamboo rafts or racks for 3 to 5 months during their growth phase. There is only one site suitable for the collection of wild spat, upon which the industry depends, and with the continual threat of coastal development and the increased demand for spat, the development of an oyster hatchery may become necessary to sustain oyster culture in Jamaica. Furthermore, a reportedly high mortality of the cultivated stock in Jamaica (up to 80%, Hanson and Alexander 1987), although less than the values reported by Nikolic and Alfonso (1971), Nikolic et al. (1976) and Bosch and Nikolic (1975), has prompted a preliminary investigation of seasonal differences in sex and condition of raft cultivated *C. rhizophorae*.

Alexander and Newkirk (1987) consider that "growth and survival of these oysters seem more related to the impact of competitive and predatory biological agents than to genetically influenced traits". Although these undoubtedly contribute to mortality (Littlewood 1987), Littlewood and Donovan (1988) argue that the ecology of *C. rhizophorae* forces it to grow fast, reproduce early and die young.

Extensive studies on the reproductive cycle of wild, predominantly intertidal, *C. rhizophorae* have been conducted in Venezuela (Vélez, 1977) and Brazil (Nascimento and Lunetta 1978, Dos Santos and Nascimento 1980, Nascimento et al. 1980a, Ramos and Nascimento 1980) and a single study on seasonal variation in condition and glycogen content is reported from Venezuela (Rojas and Ruiz 1972). However, there appears to be no data taken from cultivated or subtidally grown oysters.

The present study forms part of a series of experiments to determine factors contributing to mortality and limiting the growth of raft cultivated mangrove oysters. The same data may also serve in the development of hatchery technology for *C. rhizophorae*

MATERIALS AND METHODS

Approximately 30 oysters from each of four size classes (20–29 mm, 30–39 mm, 40–49 mm and >50 mm) were taken from a single commercial raft at Port Morant, St. Thomas (Lat. 17°35′N; Long 76°19′W) every 28 days from 13 May 1986 to 22 September 1987. The raft was restocked with young oysters every 3 to 4 months.

Oysters were taken back to the laboratory where individual shell height and whole weight were recorded. Oysters were shucked into preweighed aluminium dishes. Small quantities of gonad material were sampled with a glass pipette and sex was determined on the basis of presence of sperm or eggs. Values for sex-ratio are given by the proportion of males divided by the proportion of females.

Empty shells and meats were dried to constant weight in a fan oven held at 90°C. Dry meat weight was calculated and shell weight was recorded. The dried meats from approximately three oysters of each sex from each size class were stored for glycogen analysis. Condition index was calculated from the formula given by Walne and Mann (1975):

$$\text{condition index} = (\text{dry meat weight/shell weight}) \times 1000$$

Glycogen concentration in dried meat samples was determined with a procedure derived from Montgomery

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(1957) and Westenhouse (1968) using phenol and sulphuric acid as reagents. Dry meats were macerated in 10 ml of 30% sodium hydroxide for 30 mins at 80°C. Glycogen was precipitated overnight in 12 ml of 95% ethanol. The precipitate was further purified by alternately dissolving in boiling water and precipitating in 66% ethanol three times. The final solution of glycogen in water was made up to 20 ml and diluted by a factor of ten. To each of three replicate 2 ml samples 0.1 ml phenol and 5 ml concentrated sulphuric acid were added. After standing for 30 mins with intermittent stirring, absorbance was measured at 420 nm with a Pye Unicam SP6-450 UV/VIS spectrophotometer. At each analysis a standard absorbance curve was determined from solutions of pure glycogen. Glycogen content was expressed as mg · g^{-1} dry weight of oyster.

Spatfall data for 6 panel stations at Port Morant were provided by the Oyster Culture Jamaica Project, Ministry of Agriculture. Frosted glass panels (200 mm × 80 mm) were held in the bay at less than 1 m depth for a week at a time before spat were counted. Stations were within 150 m of the raft.

Monthly rainfall data from the three nearest Meteorological Office stations (Figure 1) were collected and plotted.

RESULTS

The sex of oysters with neither sperm nor eggs was classed as 'indeterminate'. The simple gonadal smear technique was unable to indicate the presence of any hermaphroditic individuals. Figure 2 illustrates the proportion of each sex in each monthly sample. Each bar is composed of shaded areas representing the size classes. Consequently, unlike the total height of each bar, heights of shaded areas are relative within a column and their actual values cannot be read directly from the x-axis.

Over the whole sampling period a total of 1452 females and 381 males were recorded; 498 were of indeterminate sex. The mean monthly sex-ratio over the sampling period,

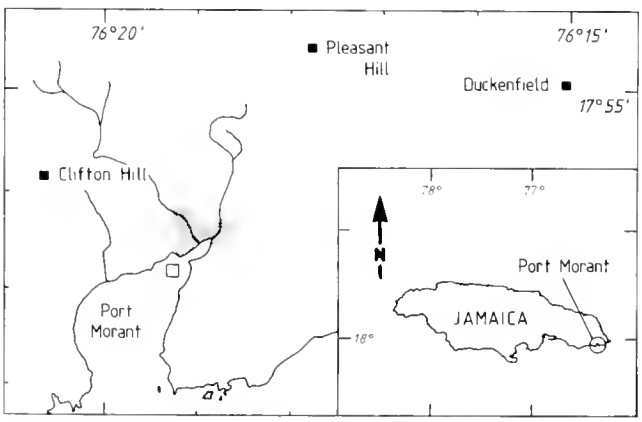

Figure 1. Map showing Port Morant and stations where rainfall was recorded (filled squares); open square in bay indicates position of raft; stippled area represents distribution of mangrove and wild *C. rhizophorae* population.

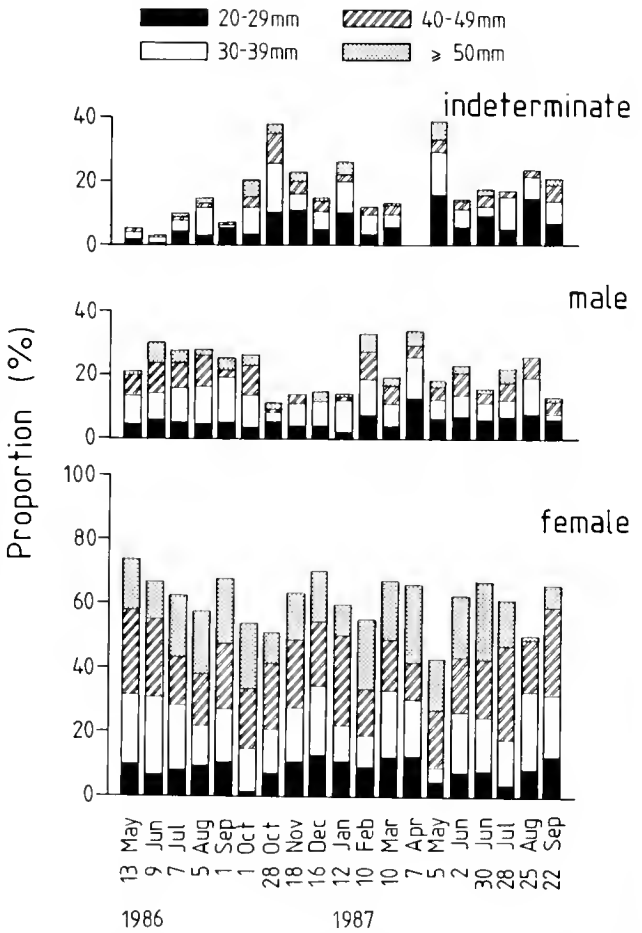

Figure 2. Proportion of indeterminate, male and female oysters. Relative proportions of each sex found in the four size classes are represented within each bar.

of approximately 3 females to 1 male (0.36 ± 0.13; mean ± SD), was largely reflected within each month. Table 1 shows overall sex-ratios for each sampling date and the results of chi-squared tests to determine whether there was a significant difference in sex ratio between size classes at each sampling date. A greater proportion of the large oysters were female throughout the sampling period.

Peaks in the overall proportion of indeterminate oysters in October 1986 and six months later in May 1987 coincided with apparent reductions in the proportion of females (Figure 2). Comparing spatfall at the same intervals (Figure 3) suggests that these may be post-spawning periods and that at least a portion of the indeterminate oysters, may be females in their recuperative phase (see Nascimento and Lunetta 1978). Although there is an apparent cyclicity in the overall proportion of females and indeterminates during the sampling period, no such trend exists for the males.

Figure 3 is a series of plots of mean glycogen concentration in males and females, overall mean condition index and spatfall. As there was no significant difference in glycogen concentration between males and females at any sampling date (ANCOVA, sampling date and shell height

TABLE I.

Overall sex-ratio and difference in sex ratios between size classes at each sampling date (chi-squared test).

Date	Overall ratio ♂/♀	df	sig.
13 May 1986	0.28	15	ns
9 Jun 1986	0.45	15	ns
7 Jul 1986	0.44	10	ns
5 Aug 1986	0.48	10	ns
1 Sep 1986	0.37	15	**
1 Oct 1986	0.49	15	ns
28 Oct 1986	0.22	10	ns
18 Nov 1986	0.22	15	ns
16 Dec 1986	0.21	15	ns
12 Jan 1987	0.24	12	***
10 Feb 1987	0.60	12	*
10 Mar 1987	0.28	12	*
7 Apr 1987	0.51	5	*
5 May 1987	0.42	12	**
2 Jun 1987	0.37	10	ns
30 Jun 1987	0.23	12	*
28 Jul 1987	0.35	10	**
25 Aug 1987	0.51	8	*
22 Sep 1987	0.19	8	ns

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns = not significant.

as covariates; $P = 0.131$) an overall mean concentration is plotted. ANCOVA, controlling for the variance due to sex and sampling date, showed that shell height had no significant effect on glycogen concentration ($P = 0.370$).

Condition indexes of males and females at each sampling date were not significantly different (ANCOVA, sampling date and shell height as covariates; $P > 0.05$). Although more data would be desirable, condition index appears to follow a seasonal cycle associated with spatfall, which in turn is associated with periods of heavy rainfall in May 1986, October–December 1986 and April–May 1987 (Figure 4).

There were three recognisable peaks in spatfall during the sampling period (Figure 3). The first and greatest occurred in June 1986. Both less pronounced, but not significantly different (t-test; $P > 0.05$), the second peaks in January and the third extends from June to August 1987. Each of these spatfalls followed periods of extended rainfall.

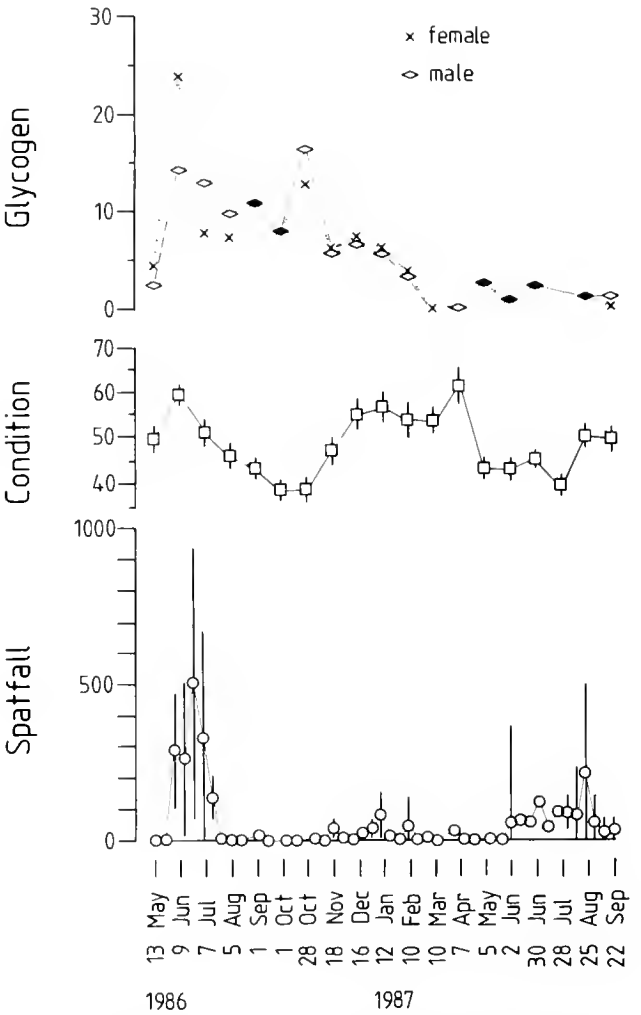

Figure 3. Glycogen content (mg · g^{-1} dry meat weight), condition index and recorded spatfall (mean number spat per panel [800 mm × 80 mm] per week) during the sampling period; means ± 95% confidence intervals.

DISCUSSION

Existing literature indicates that sex-ratio in *Crassostrea rhizophorae* is highly variable. Differences in sex-ratio reflected between different size classes, taken as a consequence of the oyster's protandrous nature, is well documented, generally consistent in trend, but inconsistent in relation to specific values. For instance, Nascimento (1978) showed that 83.5% of individuals between 40–60 mm were female. We show that within the same size range between 18.0 and 43.6% were female. Vélez (1982) studying histological sections showed that within a population of wild *C. rhizophorae* sex-ratio was maintained at approximately 1.0, Nikolic and Bofill (1971) report ratios of approximately 0.67 and Nascimento et al. (1980a) recorded a range of sex-ratios from 0.05 to 0.41. Urpí et al. 1983 report unexpectedly high sex ratios of 3.03 but offer no explanation. In the present study overall sex-ratio ranged from 0.19 to 0.60 (see Table 1). Notwithstanding variation in sex-ratio due to geographical differences, there is often little mention in the literature of seasonal changes, nor variation due to tidal range or age and size structure of the populations monitored. Consequently it would be unwise to determine how the variability mentioned above occurs by means of comparing the studies. Nonetheless it appears likely that age and size structure of the oyster populations may be the principal factor to consider. Both the wild and cultivated stock appear to be relatively small in Jamaica, compared to *C. rhizophorae* from other countries (e.g. in

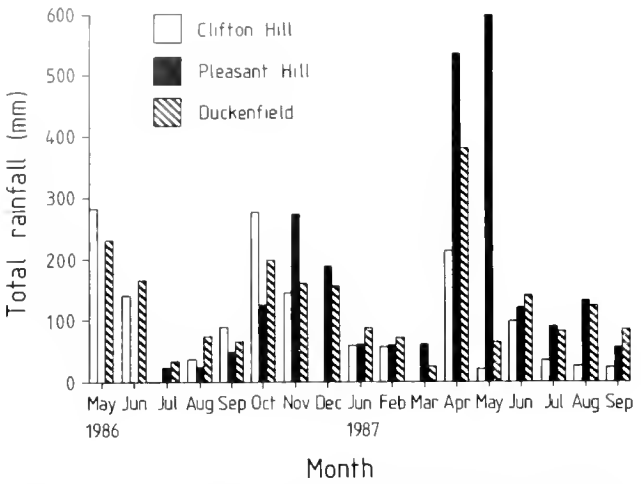

Figure 4. Total monthly rainfall (mm) recorded at Clifton Hill Estate, Duckenfield and Pleasant Hill (see Figure 1). There are no data for Pleasant Hill for May or June 1986.

Brazil, Nascimento et al. 1980a, in Cuba, Nikolic and Alfonso 1971, and in Costa Rica, Urpí et al. 1983). Smaller oysters tend to be male and with a relative shortage of larger individuals a sex-ratio closer to 1:1 may be expected. Furthermore, the oysters taken from the commercial raft are likely to have been relatively young and therefore a relatively large proportion would be male.

Crassostrea rhizophorae is a protandrous hermaphrodite, with up to 10% of individuals developing into females without passing through a functional male phase (Nascimento et al. 1980a). Although continuous spatfall of the mangrove oyster occurs all year round throughout its geographic range (e.g. Mattox 1949, Bacon 1971, Nascimento et al. 1980a), there are generally two major spatfalls each year coinciding with extreme variations in salinity and water temperature brought on by periods of heavy rainfall (Watters and Prinslow 1977, Vélez 1977, Nascimento et al. 1980b). Indeed, in Jamaica, and during the current study, spat are most abundant during the rainy seasons beginning in April and October. The prolonged spatfall agrees with the observation that gamete release is partial in this species apparently continuing for up to three months through successive spawnings (Ramos and Nascimento 1980). Nascimento et al. (1980b) suggested that intense rains of over 150 mm · wk^{-1} may actually depress gamete release and this may explain why spatfall was not as pronounced in April and May 1987 when rainfall was particularly high. Unfortunately, neither weekly rainfall nor salinity data are available to corroborate this.

Neither glycogen content nor condition index of cultivated oysters appear to be reliable predictors of spatfall at Port Morant, although the matter is complicated by the proximity of the raft held stock to the wild population. Moreover, other regional studies on variation in glycogen content of bivalves have shown that site can play an important role in concealing any seasonality despite cyclical trends in air and water temperature and rainfall (e.g. in *Ostrea arborea* Chemnitz in Brazil, Antunes and Itô 1968). Much of the spatfall recorded at Port Morant is assumed to come from the natural population amongst the mangrove and this is subjected to different biotic and abiotic factors compared to the cultivated stock (Littlewood in press). A more accurate determination of spatfall from the raft grown population therefore may be effected by holding oysters in a bay away from a wild population.

Further research may indicate whether or not the onset or likelihood of spatfall is dependent on condition, although from the present study it seems unlikely that the intensity of spatfall may be linked to either condition index or glycogen content. The intense spatfall at the beginning of this investigation coincided with a build up of glycogen content. Glycogen fell immediately after the onset of spatfall and may be explained by the dependence of vitellogenesis on stored glycogen reserves (Gabbott 1975). Reductions in mean monthly condition index appear to represent post spawning periods, as observed by Nascimento and Pereira (1980).

A statistically significant relationship between condition index and glycogen content in *C. rhizophorae* was demonstrated for a wild population in Venezuela (Rojas and Ruiz 1972). Although the indexes of conditions are different, it is felt that the ratio of dry meat weight to shell weight used in the present investigation, recognised for its value as an indicator of physiological condition (Lucas and Beninger 1985), is not responsible for a lack of relationship. Indeed, the decline in glycogen content during the months of October 1986 to April 1987 which coincided with a gradual increase in condition index, may be explained by the conversion of glycogen into lipid reserves of the developing eggs during a 'storage cycle' (cf. *Mytilus edulis* L., Gabbott 1975). An increase in gonadal production and storage would be reflected in the dry weight of the oysters and hence condition index. Release of these stored gametes may have occurred during the second major, prolonged spatfall beginning in June 1987. An analysis of histological sections taken during the course of the present investigation may provide suitable evidence for this scenario. However, the same scenario cannot explain the coincident peaks in condition and glycogen content preceding the first spatfall.

ACKNOWLEDMENTS

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SEASONAL ABUNDANCE OF OYSTER SPAT AND FOUR ANIMAL ASSOCIATES ON AN OYSTER REEF IN THE JAMES RIVER, VIRGINIA.[1]

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ABSTRACT Five species of invertebrates collected at bi-weekly to monthly intervals from an oyster reef in the James River, Virginia, between September 1984 and August 1985 exhibited similar patterns of fluctuation in abundance throughout most of the period. The species were: spat of the oyster *Crassostrea virginica;* two species that feed on oysters, the flatworm *Stylochus ellipticus*, and the gastropod *Boonea impressa*, as well as two others with no known direct trophic interactions with the oyster, the isopod *Cassidinidea lunifrons* and the nudibranch *Doridella obscura*. *B. impressa* was many times more abundant than *S. ellipticus* but because of the difference in feeding habits between the two species it is speculated that *S. ellipticus* has a greater harmful effect on oysters than its abundance would suggest. Densities of all species declined sharply between early October and early November; the decline was probably related to seasonal mortality associated with declining water temperatures. *B. impressa* and *C. lunifrons* were the most abundant species throughout most of the sampling period, but only oyster spat showed a definite high peak in recruitment in 1985. Failure of the data to show reproduction peaks for three of the other species was attributed to incomplete retention of smaller individuals in the 0.5 mm-mesh screen used; large variations in density did not permit clear definition of a peak in *C. lunifrons*. It is recommended that studies of oysters on their reefs include other abundant noncommercial species to provide a stronger foundation for management of the resource than if only the oyster was studied.

KEY WORDS: seasonal abundance, *Crassostrea, Stylochus, Boonea, Cassidinidea, Doridella*

INTRODUCTION

Reefs and beds of the American oyster *Crassostrea virginica* (Gmelin 1790) harbor a great variety of organisms which form recognizable assemblages (Wells 1961, Larsen 1974a, 1985). Several animals in those assemblages have direct trophic interactions with the oyster; among these are the ectoparasitic pyramidellid gastropod *Boonea impressa* (Say 1822) and the predatory polyclad turbellarian *Stylochus ellipticus* (Girard 1850). Although these species are not entirely dependent on oysters as host or prey, they reduce oyster growth and survival (Loosanoff 1956, Provenzano 1959, Landers and Rhodes 1970, Leathem and Maurer 1975, Robertson and Mau-Lastovicka 1979, White et al. 1984, Ward and Langdon 1986).

Knowledge of the nature and magnitude of the effect of *B. impressa* and *S. ellipticus* on oyster populations is necessary for proper management of that resource and quantification of their seasonal abundance is important because time and extent of changes in their abundance would have a direct impact on survival of oyster spat. The original objective of this study was to estimate the abundance of oyster spat, *B. impressa* and *S. ellipticus* on an oyster reef over one year. Two other species, the isopod *Cassidinidea lunifrons* and the nudibranch *Doridella obscura*, were subsequently included in the study when their consistent incidence in the samples became evident.

The study was conducted at Wreck Shoal, a subtidal oyster reef in the James River, Virginia. The James River estuary provides the oyster industry in Virginia with most of its supply of seed oysters and Wreck Shoal has been one of the most productive reefs in that estuary (Haven and Whitcomb 1983).

MATERIALS AND METHODS

Wreck Shoal is located between the navigation channel and the northeast shore of the James River, approximately 29 km from the river mouth at Old Point Comfort, in the mesohaline zone of the estuary. Water depth at mean low water over the reef ranges from 1.8 m near shore to 5.5 m near the channel. Our sampling site was located 200 m from the channel (Lat. 37°03.2′ × Long. 76°34.6′) close to sampling site 4 of Larsen (1974a, 1985). The site was divided into 40 plots of 57-m^2 each; five randomly-selected plots were sampled at bimonthly or monthly intervals between September 1984 and August 1985.

Samples were collected using a portable suction sampler designed for use on the hard shelly substrate of oyster reefs (Larsen 1974b). The area covered by the sampler was 0.013 m^2. The material lifted by suction accumulated in a collection bag with a mesh size of 0.5 mm. Each sample was transferred from the bag to a 4% solution of ethanol in river water for relaxation of the animal specimens. Subsequently they were fixed in 4% formalin, washed through a series of sieves (4.0, 2.0 and 0.5 mm,) and stored separately in 70% ethanol with Rose Bengal. Some of the col-

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lections were sieved through an additional screen with a mesh size of 0.25 mm.

Only spat of *Crassostrea virginica* under 20 mm in shell height were included in the study because we were primarily interested in the younger members of the oyster population. Unpublished data collected earlier by one of us (R.M.-A.) showed that newly settled spat at Wreck Shoal did not grow to a height greater than 20 mm in one year. Xanthid and portunid crabs were rare in our samples, possibly because they could evade collection; therefore, we do not present any data for those taxa. Densities of the other organisms are expressed in m^{-2} and 94% confidence intervals are provided.

Nonparametric statistical methods were used in data analysis because of frequent skewed distributions. The median number of animals in the five samples collected on each date was computed as the Hodges-Lehman point estimator associated with Wilcoxon's rank statistic and based on Walsh averages (Hollander and Wolfe 1973). A symmetric two-tailed confidence interval for the median was also computed using a procedure attributed to Tukey (Hollander and Wolfe 1973). The small number of samples limited determination of the confidence interval to a probability level of 93.8%. The upper and lower confidence limits actually corresponded to the range in density for each species on the given date.

Overlap of the median for one sampling date or species by the confidence interval of an adjoining median was assumed to be an indication that a statistical difference would not likely be detectable at the given probability level (McArdle 1987). Lack of an overlap was assumed to be an indication that existence of a significant difference between the two medians was very probable. No other statistical analyses were warranted because of the large variances and lack of variance homogeneity among many of the samples.

RESULTS

Two easily recognizable animals not included in our original study plan were found consistently in our samples. They were the dorid nudibranch *Doridella obscura* Verril 1870 and the flabellarid isopod *Cassidinidea lunifrons* Richardson 1905. Although there was no indication that these two species had any direct impact on survival and growth of oyster spat, they were added to the study because their constancy and abundance suggested a close association with the oyster reef.

Two types of polyclad turbellarians in the collections were readily distinguished from each other by their shape. One was identified as *Euplana gracilis* (Girard 1850), an elongate flatworm previously reported from the mesohaline and oligohaline zones of the James River (but not from Wreck Shoal) by Larsen (1974a). We only found seven specimens of this species in two samples (four on September 20 and three on October 4) and will not consider it further.

The second type of flatworm was assumed to be *Stylochus ellipticus* (Girard 1850) because separation of *S. ellipticus* from a similar species found in Chesapeake Bay, *Coronadena mutabilis* (Girard 1850), was hindered by the condition of the specimens following preservation. *C. mutabilis*, however, has never been found at Wreck Shoal (J. P. Whitcomb personal communication) and has been reported previously only from higher salinity zones (Lawler 1969, Marsh 1970, 1973, Wass 1972, Andrews 1973, Orth 1976). Although Faubel (1983) proposed that *Stylochus ellipticus* be moved to the genus *Stylochopsis* Verrill 1873, we have chosen to retain the earlier taxonomic combination.

Some of the collections sieved through an additional 0.25 mm screen showed that as many as six times the number of flatworms, twice as many gastropods and an equal number of *D. obscura* were retained in the 0.25 mm screen as were retained in the 0.5 mm screen. The number of *C. lunifrons* was 17 times higher in the 0.5 mm screen as in the 0.25 mm screen. We, however, were not able to modify our sampling design to account for those findings. Oyster spat, which were attached to shells and shell fragments, were easily retained in the large-mesh screens.

The five species included in our study (*Crassostrea virginica, Boonea impressa, Stylochus ellipticus, Cassidinidea lunifrons* and *Doridella obscura*) were present in the samples on all dates (Table 1). Variation in species-specific density between replicate samples was high (Figures 1 and 2, Table 1). A similar pattern was, nevertheless, evident in the seasonal abundance of the five species over time. Their numbers were highest in early October, decreased sharply in late October and, except for a slight peak in mid-November, remained at approximately the same level through May 1985.

Only *C. virginica* spat showed a significant increase in numbers attributable to recruitment through reproduction after May. There was an indication of an increase in abundance of *C. lunifrons* in August but the large variation in numbers prevented any attribution of significance to the increase.

B. impressa was by far the most abundant of several pyramidellid species in our samples (Cox & McCarthy 1987, MS in preparation); median density was consistently high, ranging between 3100 and 6200 m^{-2} except for a depression to about 1937 m^{-2} in mid-October and early November (Figure 2). Median densities of *B. impressa* and *C. lunifrons* were similar in magnitude in 1984 and were substantially higher in most instances during that period than those of *S. ellipticus* and *D. obscura*. Densities of *S. ellipticus, C. virginica* spat and *D. obscura* were similar throughout the year except in July 1985 when newly-settled oyster spat appeared in the collections.

In 1985, median densities of *B. impressa* were higher than those of the other species except in March and August when no difference was apparent between its density and

TABLE 1.

Total number of individuals of five species of invertebrates in samples collected between September 1984 and August 1985 from the oyster reef at Wreck Shoal in James River, Virginia. Values are for total of five samples on each date that added to an area of 0.065 m^{-2}. Range in number among samples is given in parentheses.

Coll. Date	*Crassostrea virginica* Spat	*Boonea impressa*	*Stylochus ellipticus*	*Cassidinidea lunifrons*	*Doridella obscura*
1984					
Sep 20	111 (16–35)	298 (11–136)	75 (3–35)	520 (44–274)	35 (1–21)
Oct 4	162 (16–58)	451 (45–231)	105 (6–44)	637 (61–298)	180 (20–62)
19	41 (3–12)	168 (11–79)	38 (3–19)	188 (21–60)	49 (1–14)
Nov 1	16 (2–5)	122 (2–55)	27 (1–10)	96 (10–38)	15 (1–8)
15	56 (6–21)	304 (45–86)	45 (4–15)	254 (32–71)	25 (2–8)
28	21 (1–8)	190 (14–65)	23 (0–10)	123 (11–40)	22 (1–8)
Dec 11	30 (4–7)	236 (7–82)	32 (0–13)	143 (9–44)	56 (2–23)
1985					
Jan			(No Collections Made)		
Feb 11	22 (0–9)	382 (36–131)	34 (0–16)	170 (11–58)	134 (0–42)
Mar 13	29 (3–9)	181 (8–57)	9 (0–3)	155 (2–58)	40 (1–14)
Apr 23	10 (1–3)	338 (56–91)	4 (0–2)	187 (1–72)	43 (1–29)
May 30	13 (1–5)	229 (37–57)	32 (0–16)	73 (10–24)	52 (1–21)
Jul 18	653 (22–281)	378 (56–102)	32 (1–12)	215 (3–63)	56 (5–20)
Aug 13	237 (28–109)	301 (13–118)	16 (0–9)	740 (13–492)	32 (0–20)

that of *C. lunifrons*. The greatest range in median density during the 12-month period was shown by *C. lunifrons* and *C. virginica* spat primarily because of the high numbers in the summer of 1985.

Bottom water temperature at Wreck Shoal in 1984 was at its peak (28.7°C) in mid-August 1984 but declined steadily to 14°C by the end of October and reached a low of 4°C in February 1985 (Figure 3). From February onward it increased steadily through August 1985. Temperatures recorded between August and December 1984 and between June and August 1985 were similar to those recorded by others at the same station in 1982, 1983 and 1986. Bottom water salinity fluctuated between 11 and 16‰ from June to November 1984 except for a low point of 6.7‰ on August 23 (Figure 4A). It was lower than recorded for that period in the previous two years and in the following two (Figure 4A and B). In 1985 salinity was above 14‰ after March and from July to October it was between 17 and 19‰ except for a sharp decrease to 9.7‰ in late August.

DISCUSSION

Densities of the five species included in this study were characterized by large variations among samples collected on the same date. Differences in bottom texture (i.e., relative concentration of shells and oysters) within the oyster reef were probably the primary factor responsible for those variations. Earlier investigations showed that the density of benthic epifauna increased with increases in concentration of shelly substrate (Barnes et al. 1973, Dauer et al. 1982, Larsen 1974a, 1985). In his study of James River oyster reefs, Larsen (1974a, 1985) reported differences in bottom texture between reefs separated by distances of several kilometers while Haven and Whitcomb (1983) and De Alteris (1986) described differences within the same reef. Underwater observations by divers conducting research at our work site revealed that the differences were evident within distances of a few meters. In spite of the large variations in numbers of animals between samples, similar seasonal abundance patterns were evident among the species studied.

These species are consistent components of the oyster reef assemblage and thus, probably share similar ecological requirements, biological interdependencies and adaptations to the physical conditions of that habitat in the sense suggested by MacGinitie (1939), Swartz (1972) and Roughgarden and Diamond (1986). The four species other than the oyster included in this study do not depend exclusively on the oyster for their food nor are they found exclusively on oyster reefs (Allen 1958, Landers and Rhodes 1970, Larsen 1974a, Orth 1976, Schultz 1978, Maurer et al. 1979). They do find, however, an abundant supply of their preferred prey in the oyster reef: barnacles, oysters and other molluscs for *B. impressa* and *S. ellipticus* (Allen 1958, Landers and Rhodes 1970) and encrusting bryozoans for *D. obscura* (Franz 1967, Perron and Turner 1977, Todd 1981). We found no reference in the literature to food preferences of *C. lunifrons* but Schultz (1969) stated that most free-living marine isopods are scavengers; as such this species should not lack for food in the oyster reef.

The consistently high abundance of *Boonea impressa* throughout the year could be a significant factor in its potential impact on *Crassostrea virginica* spat and juveniles. Wells (1959) and White et al. (1984) reported that reproduction and recruitment of *B. impressa* in North Carolina and Texas occurred more or less continuously throughout the year. White et al. (1984) also found that oyster popula-

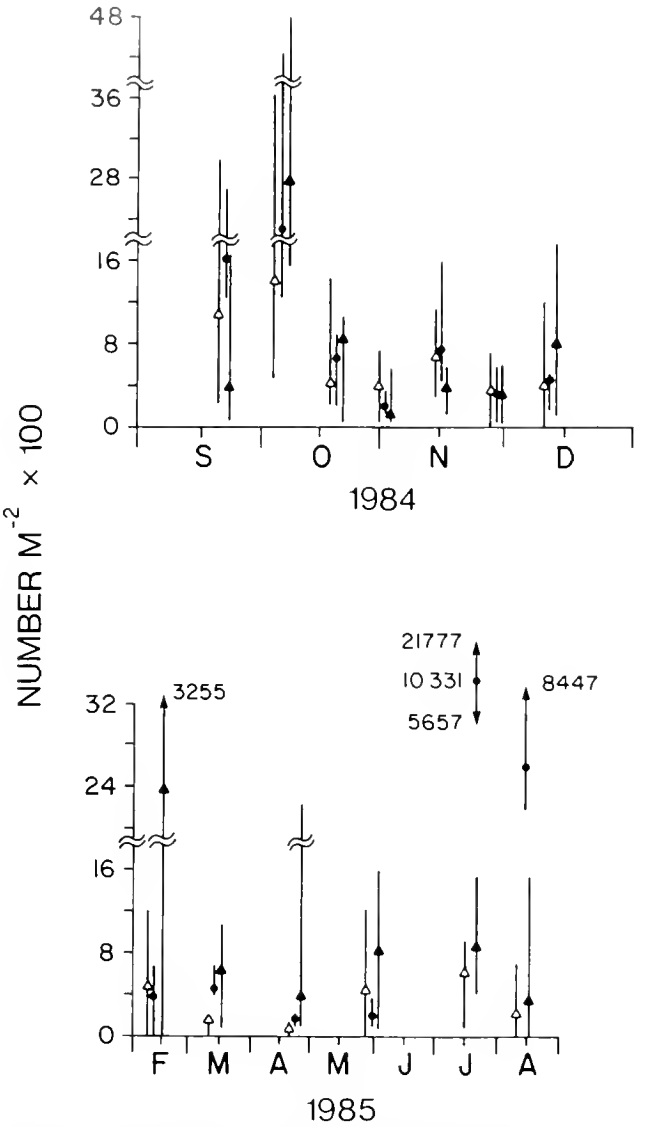

Figure 1. Median density and 94% confidence interval for samples of *Crassostrea virginica* spat <20.1 mm (●), *Doridella obscura* (▲) and *Stylochus ellipticus* (△) collected at Wreck Shoal, James River, Virginia, between September 1984 and August 1985.

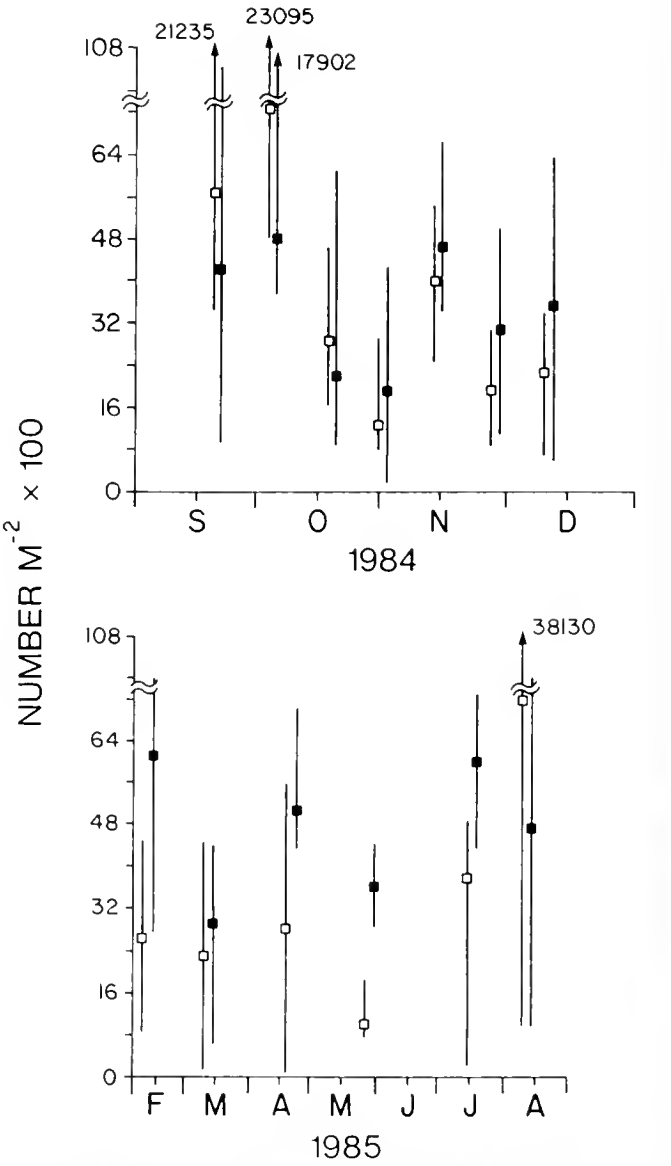

Figure 2. Median density and 94% confidence interval for samples of *Boonea impressa* (■) and *Cassidinidea lunifrons* (□) collected at Wreck Shoal, James River, Virginia, between September 1984 and August 1985.

tions were parasitized by *B. impressa* at all times of the year. The same may be true (except perhaps for the colder winter periods) in James River reefs harboring this gastropod as indicated by the persistent high densities observed at Wreck Shoal.

Though *S. ellipticus* densities were much lower than those of *B. impressa*, their impact on oysters may nevertheless be greater than numbers alone would suggest. Predation by *S. ellipticus* is certain to cause the death of its oyster prey (Provenzano 1959) while the parasitic effect of *B. impressa* is unlikely to be fatal and tends to be transitory (White et al. 1984). Although the actual impact of *B. impressa* and *S. ellipticus* on survival of oyster spat has not been quantified, the magnitude of their densities on Wreck Shoal are sufficiently high to raise concern about their potential harmful effect on new recruits to the oyster population.

The most notable change in abundance among the species studied was the sharp reduction observed in October 1984. We interpret this as a mortality event because no consistent recovery in numbers was evident in the succeeding months; the mortality was probably associated with the seasonal decrease in water temperature recorded at that time. Water salinity in 1984 was not unusually low when compared with long-term annual and seasonal averages of 12–14% given by Andrews (1973), Larsen (1974a), Haven and Whitcomb (1983).

The large number of flatworms, gastropods and nudi-

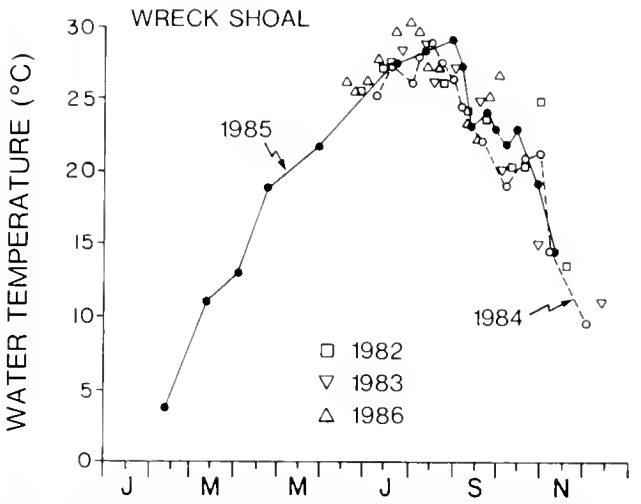

Figure 3. Bottom water temperature on given dates for period 1982–1986 at Wreck Shoal, James River, Virginia.

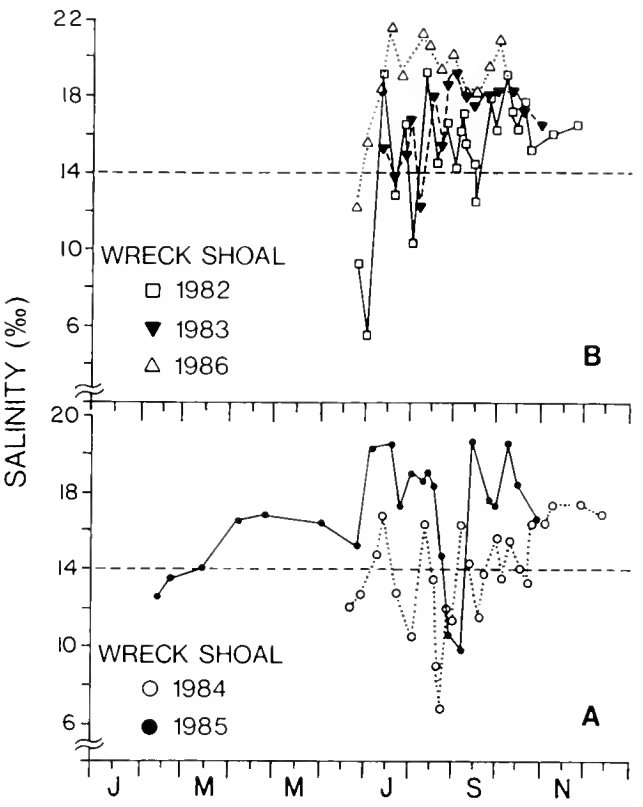

Figure 4. Bottom water salinity on given dates for period 1982–1986 at Wreck Shoal, James River, Virginia.

branchs that passed through the 0.5 mm screen in collections sieved through an additional 0.25 mm screen indicates that many of the smaller individuals of those populations were excluded from our data. The actual numbers were probably even higher than those retained in the 0.25 mm screen because many may have already been lost through the 0.5 mm mesh of the sampler collection bag. The oyster was the only species with a clear peak in recruitment in 1985; that peak occurred in July. Inasmuch as the oyster was the only species not affected by the choice of screen size, the absence of distinct recruitment peaks of the other species in 1985 could be attributed to loss of the smaller individuals through the 0.5 mm screen. Our experience during this study emphasizes the need to use a 0.25 mm screen in future studies of oyster reef epifauna as was recommended by Maurer and Watling (1973) and McLusky (1981).

This study has shown evidence of a close relationship in seasonal fluctuations in abundance of oyster spat and four other major members of the faunal assemblage on an oyster reef. We have at present very little knowledge about the life history and ecological relationships of most of the organisms that share the oyster reef habitat. Oyster associates on the reef most likely depend on the oyster to a greater extent than the oyster depends on them (Puffer and Emerson 1953, Andrews and Wood 1967, Boesch 1971, Maurer and Watling 1973, Dayton 1984). Most of them are small annual species and are subject to great variations from year to year because they are more susceptible to environmental changes than are larger species (Thorson 1957, MacArthur and Connell 1966). An extended absence or depressed abundance, however, of species associated with the oyster on the reefs may forecast conditions potentially harmful to the oyster population.

Studies that include the non-exploited species in an ecosystem containing a commercially valuable species are not usually undertaken by managers of natural resources and their scientific advisors even though they may provide a more solid foundation for future management decisions than studies that exclude those species (May 1984). Therefore, it appears advisable to include all or most of the major components of the oyster reef assemblage in future studies of that ecosystem as was implied by Andrews and Wood (1967) and Carriker (1967) and suggested by Swartz (1972) and Maurer and Watling (1973).

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AN INDIRECT METHOD FOR ESTIMATING LONGEVITY OF THE HORSESHOE CRAB (*LIMULUS POLYPHEMUS*) BASED ON EPIFAUNAL SLIPPER SHELLS (*CREPIDULA FORNICATA*)

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ABSTRACT The large, sessile gastropod, *Crepidula fornicata*, is frequently found encrusting the carapaces of sexually mature horseshoe crabs, *Limulus polyphemus*. A technique for approximating the age structure of an adult crab population based on these encrusting organisms is described. *Crepidula* over 5 cm in length were found attached to horseshoe crabs; these were estimated to be at least 8 years old, based on equations derived from Walne (1956). This would suggest that the crab host had not moulted for at least that length of time. Attempts to validate *Crepidula* age using internal shell structure were inconclusive, although microgrowth increments of undetermined periodicity were observed in the shell septum. Since horseshoe crabs may attain ages of 9 to 11 years before moulting ceases, the data indicate that a maximum age of at least 17 to 19 years is reached by horseshoe crabs of both sexes.

KEY WORDS: horseshoe crab, *Limulus*, age, *Crepidula*, growth

INTRODUCTION

Relatively little is known about age and growth in horseshoe crabs despite extensive biomedical uses (Cohen 1979, Pearson and Weary 1980, Novitsky 1984), its use as bait in commercial eel and whelk fisheries (Botton and Ropes 1987a), its role as a predator of commercially important bivalves (Botton 1984a, b, Botton and Haskin 1984), and the importance of its eggs in providing food for migratory shorebirds (Botton 1984c, Myers 1986). Estimates of growth rate and longevity of *Limulus polyphemus* (L.) are based on anecdotal observations. The often-cited figure that horseshoe crabs require 9–11 years to reach adult size in the middle Atlantic region is based on a series of exuviae from a single captive specimen (Shuster 1950). Longevity has been demonstrated to be at least 5 years beyond the terminal moult (Ropes 1961), based on the recovery of a tagged adult 5 years after release in Plum Island Sound, Massachusetts. Animals in the Gulf of Mexico may reach sexual maturity more rapidly (Wells et al. 1983) and attain a smaller maximum size than in the middle Atlantic region (Shuster 1979).

An evaluation of the age structure of sexually mature adults is an important component of ongoing studies of horseshoe crab population dynamics in Delaware Bay (Botton and Loveland in preparation) and the middle Atlantic continental shelf (Botton and Ropes 1987a, b). Analysis of age structure using size-frequency distributions has thus far failed to resolve the expected number of age classes, suggesting that crabs of the same carapace width may be of different ages. There are no known structures in horseshoe crabs, analogous to bivalve shells or fish otoliths, which can be used for direct determination of age. However, carapaces of adult horseshoe crabs are frequently encrusted by epifaunal invertebrates, some of which, including barnacles, blue mussels, and slipper limpets, could potentially be useful in approximating ages of adult horseshoe crabs.

Because of their prevalence on horseshoe crab carapaces, and their large size, the slipper limpet, *Crepidula fornicata* (L.), was evaluated as an indirect indicator of the age of an adult crab. This methodology is based on three assumptions, that:

1. Either adult horseshoe crabs have a terminal adult moult, or moulting of adults is an extremely rare phenomenon;
2. *C. fornicata* attach soon after metamorphosis from the plankton and do not move, as large adults, onto the carapace of a horseshoe crab; and
3. The ages of *C. fornicata* can be determined with reasonable accuracy.

The presence of a 5-year old slipper limpet would indicate, for example, that it has been at least 5 years since the crab's last moult.

The evidence for assumption 1 is twofold. First, adults have not been observed moulting; nor have adult-sized exuviae been found either during the spring spawning period, or during offshore dredge and bottom trawl operations throughout the year. Second, many carapaces are heavily encrusted with various invertebrate species (e.g. Pearse, 1947), which would not be the case if moulting occurred

*Deceased.

regularly. Fouling is far less common among juveniles (Barthel, 1974). This is not to assert that adults never moult, as it has been witnessed at least once (Lockwood 1884). Large sized crabs with soft exoskeletons are occasionally dredged from the continental shelf (Botton and Ropes unpublished data), so a small number of horseshoe crabs evidently undergo ecdysis after reaching maturity.

The second assumption, on the sessile nature of *Crepidula fornicata,* is supported by several authorities. Members of the genus *Crepidula* are protandrous hermaphrodites (Hoagland 1977). Small males are mobile and may shift substrate in search of conspecifics. Upon attaining the female phase (after the animal's first winter, but earlier if the males are isolated), the shells become immobile (Coe 1942). Full-sized solitary males are also sessile (Conklin 1898). *C. fornicata* forms permanent clusters or chains; the lowermost (oldest female's) shell is closely fitted to the rock or shell to which it is attached (Orton 1912, Hoagland 1979). Likewise, limpet shells take on the curvature of the horseshoe crab carapace. Selective advantages for adult *C. fornicata* to remain firmly attached include proximity to mates, precise fitting of shells to substrate topography, and protection against crab predation (Hoagland 1979).

The third assumption of the methodology was that the ages of *Crepidula fornicata* could be estimated. External shell growth bands are potentially useful in molluscan age determination, but based on the literature, we considered that this method would be imprecise. Coe (1942) believed that whenever a small *Crepidula* moves to a new location or is disturbed enough to withdraw the mantle, a "growth ring" forms. Sex transformation may also result in an external band. Sex change may be, in some populations, recorded as a change in the slope of the shell or a crowding together of growth lines, but "these clues cannot be relied on in all cases to separate adult females from the rest of the population" (Hoagland 1977:356). Shell length and shape in *C. fornicata* are dependent upon the characteristics of the substrate (Conklin 1898). Coe (1942) separated "narrow" growth forms characteristic of muddy or sandy sediments, from "broad" growth forms which had an unrestricted space for growth. The size and shape of the substrate affects the maximum attainable size, and shells of the same age may be of different size. Previous authors have not, however, examined growth characteristics of *C. fornicata* growing on horseshoe crab carapaces.

In a comprehensive study of *C. fornicata* from the River Crouch, England, Walne (1956) determined ages by length-frequency analysis of separate cohorts. By this method, the larger sized limpets, approximately 4 cm length, were shown to be 7 years old; this estimate was validated by repeated length measurements of marked and recaptured individuals. Sheldon (1967), using relationships between shell weight and external growth lines, deduced an 8 year maximum age for River Crouch limpets, although his assumption that external growth rings were annuli was not validated.

In evaluating our three assumptions, we feel it is justified to assume that most horseshoe crabs cease moulting after attaining adult size. *C. fornicata* probably colonize horseshoe crab carapaces while in their most mobile phase (young males, at most 1 year old but probably still in their first summer). To estimate the age of a limpet, two approaches were used:

1. Direct estimates based on length-weight-age relationships from the literature (Walne, 1956; Sheldon, 1967), and
2. Examination of internal shell growth lines (e.g. Rhoads and Lutz, 1980).

The coiling of most gastropods has limited the application of the latter method to a few uncoiled species (e.g. *Patella vulgata:* Antoine and Quemerais-Pencreac'h 1980) or to the growing margin of the shell (Williamson and Kendall 1981, Ekaratne and Crisp 1982, 1984). We applied these techniques to slipper limpets, whose nearly uncoiled growth form permits a linear cut along the principal axis of shell growth.

MATERIALS AND METHODS

Samples of *Crepidula fornicata* were obtained in spring 1984 (n = 14) and 1986 (n = 27) from carapaces of adult horseshoe crabs collected from the Cape May, New Jersey, shore of Delaware Bay. Sexual maturity in crabs was confirmed by the characteristically modified pedipalp in males, and by large size and/or presence of mature ova in females. We attempted to minimize variability in shell form by selecting *C. fornicata* growing on relatively unrestricted sections of the carapace, such as the posterior portions of the dorsal prosoma and opisthosoma. We rejected highly arched or unusually proportioned *C. fornicata,* and those showing unusual signs of wear. A third group of limpets was collected from rounded stones, approximately 5 to 10 cm along the widest dimension, which were sampled by snorkeling in shallow (<2 m) water off Stony Beach, Buzzard's Bay, Massachusetts (n = 60) in summer, 1985. These populations will be abbreviated as DB84, DB86, and BB, respectively. Shell length, width, and height (sensu Hoagland, 1977) were measured to the nearest 0.1 mm using vernier calipers (Figure 1). Shells were dried to constant weight after removal of the visceral mass, and weighed to the nearest 0.01 gm.

Reference data for length-shell weight and length-age were obtained from Walne (1956). His sample population was selected from clusters growing free on the bottom, which showed less variability in shell form than other sources. To determine whether Walne's length-age relationships would be appropriate for the DB84, DB86 and BB populations, we first determined whether the populations differed significantly in their shell length-shell weight relationships. For each population, and for Walne's reference

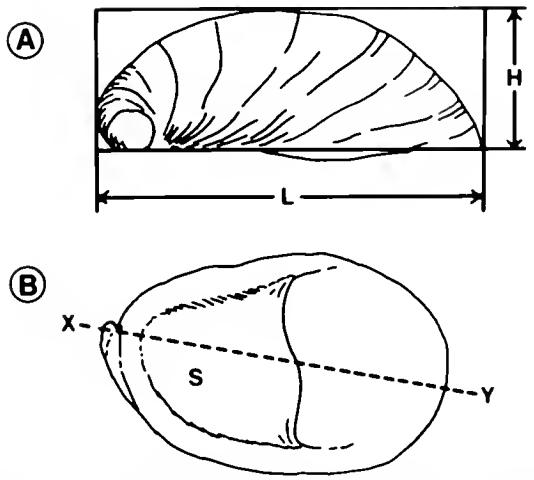

Figure 1. A. Side view of *Crepidula fornicata* showing measurement of length (L) and height (H); width is the third dimension into the plane of the paper. B. Ventral view of *C. fornicata* showing septum (s); line XY indicates direction of cut made to expose internal shell growth lines. After Hoagland (1977).

data, we computed the linear regressions of log(shell weight) versus log(length), following the general model:

$$\log w = \log a + b \log L$$

where w is shell weight, l is shell length, log a is the intercept of the line on the Y-axis, and b is the regression coefficient (Bagenal 1978). This procedure was used because the untransformed plot of length vs. weight was non-linear, and the plotting of residuals for the untransformed data indicated that a logarithmic transformation would be appropriate (Zar 1974:223). We then performed an Analysis of Variance (ANOVA) of the regression coefficients over groups, to determine whether there were significant differences between *C. fornicata* populations. A non-significant F-statistic (alpha = 0.05) from the ANOVA would suggest that the populations had similar growth characteristics, which might justify the application of Walne's length-age model to generate predicted ages for *C. fornicata* from the other populations.

Crepidula from DB84 and BB collections were prepared for analysis of internal shell microstructure following Ropes (1987). In brief, these methods entail

1. Cutting the shell with a low speed saw along the principal axis of shell growth (Figure 1);
2. Removing the periostracum by placing specimens in full strength bleach;
3. Embedding the cut surface of the shell in epoxy resin;
4. Grinding the embedded cut shell on three successively finer grits (240, 400, 600) of wettable carbide paper;
5. Polishing the specimen on a vibrating gen-polishing machine;
6. Etching the polished cut edges by immersion in 1% HCl for 1 minute; and
7. Preparing acetate peels from polished/etched shells. Peels were examined and photographed under a light microscope.

RESULTS AND DISCUSSION

Length-Weight and Length-Age Relationships

Shell length and shell weight showed a strong positive linear relationship when both variables were log-transformed (Figure 2). The only population having an r^2 of less than 0.9 was DB86, but these large specimens had a far narrower size range than the other populations (Table 1). Slope and intercept were computed for each linear regression and for all populations pooled as a single group. These parameters, compared by ANOVA, did not differ significantly over groups, although statistical significance was approached ($p = 0.105$; Table 2). This indicated that *C. fornicata* from different estuaries and substrate types had similar shell length-shell weight relationships, although without further investigation it is not possible to conclude that the rates of shell accretion are the same. The shell length-age relationships developed by Walne (1956) for River Crouch limpets were applied to those encrusting and carapaces of horseshoe crabs, with the following cautions:

1. The similarity of shell length-shell weight regression parameters across populations may suggest, but does not prove, a similarity in shell length-age relationships; and
2. Differences in nutrient regimes in the three estuaries, or between years, may affect the growth rates of *C. fornicata*, introducting a possible source of error in the age determinations.

Based on Walne (1956, his Figure 10), shell length and age were related by the equation:

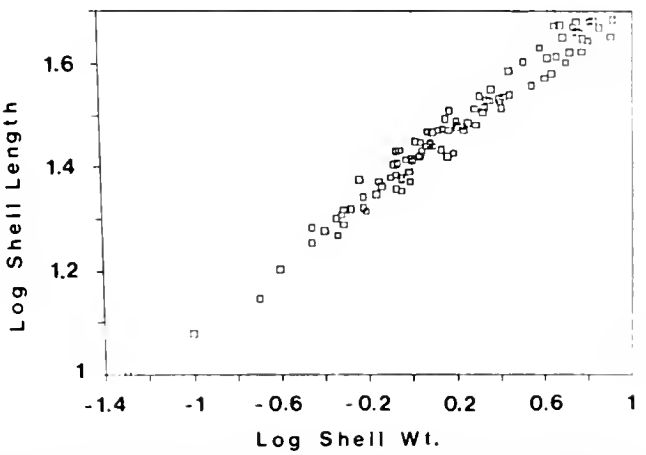

Figure 2. Relationship between log shell length (Y) and log shell dry weight (X) for all *Crepidula fornicata* populations pooled as a single group ($r^2 = 0.972$). Se Table 2 for regression parameters for each of the four source populations.

TABLE 1.

Shell length and weight statistics and linear regression parameter estimates derived from log (shell weight) vs. log (shell length) relationships for different populations of Crepidula fornicata.

Population	DF	R^2	P	Intercept	Standard Error	Slope	Shell Length (mm) Min	Shell Length (mm) Max	Shell Weight (gm) Min	Shell Weight (gm) Max
Walne	16	0.993	<.0001	−4.484	0.067	3.205	10.0	44.0	0.05	6.30
BB	58	0.931	<.0001	−4.151	0.104	2.944	18.6	41.1	0.35	4.54
DB84	9	0.974	<.0001	−4.056	0.158	2.900	20.7	48.3	0.62	8.12
DB86	8	0.327	0.084	−3.598	1.325	2.611	40.2	48.1	3.22	6.63
All data	97	0.972	<.0001	−4.259	0.052	3.023	10.0	48.3	0.05	8.12

W = Walne (1956, River Crouch, England), BB = Buzzards Bay, 1985, DB84 and DB86 = Delaware Bay 1984, 1986. Data for shells >49 mm were not included.

$$\text{Log(Age)} = -0.090 + 0.021(\text{Length}) \; (r^2 = 0.95)$$

This equation was used to calculate the age of the large limpets found on horseshoe crabs. Since Walne (1956) and Sheldon (1967) did not determine ages for animals larger than 48 mm or 8 gm, respectively, it is invalid to extrapolate ages for those individuals from DB84 and DB86 which exceeded these values. *C. fornicata* of 48 mm were approximated as 8 years old using this technique. Although not included in the regression models (Table 1), limpets as large as 59 mm were collected from horseshoe crab carapaces. These were conservatively estimated as 8+ years old, possibly as old as 11 to 13 years if the regression model is extrapolated to this length. This is consistent with a maximum age of 14 years, derived by Orton (1912) by counting the number of individuals in a chain, and assuming one individual was added to a chain each year.

Internal Shell Growth Patterns

Notwithstanding the report of Ekaratne and Crisp (1982) that shells of *C. fornicata* had no well-marked internal growth lines, microscopic growth increments were discernable in acetate peels from both BB and DB84 populations (Figure 3). However, these bands were thin, indistinct, and in our judgment, not reliable as a method of age determination. Routine and rapid counting of bands, as is done with many bivalves, does not appear feasible. Further work would be required to determine if these growth bands in *C. fornicata* are deposited annually, or in response to other events such as sex reversal or disturbance. In general, however, there appeared to be fewer than the expected number of growth lines; shells of about 4 cm length, which were estimated to be 5 to 6 years old based on the shell length-age analysis (above), generally showed only 2 or 3 distinct bands.

Very fine growth increments were observed in the septum (shelf) of *C. fornicata* (Figure 4). These microgrowth lines were seen in large as well as in 6–10 mm specimens collected just after settlement in August, 1985. The spacing between bands was variable, possibly reflecting growth conditions. Their large number suggests that they may be daily rings, and there is at least superficial resemblance between these microgrowth bands and those found in other molluscs (e.g. Jones and Crisp 1985). Even if validated, however, it would not seem practical to determine the ages of older individuals because of the time required to count the large number of rings in each shell.

TABLE 2.

Analysis of Variance of regression coefficients over different populations of Crepidula fornicata.

Source	SS	DF	MS	F	p
Total	0.483	97			
Regression over groups	0.052	6	0.009	1.815	0.105
Residual within groups	0.431	91	0.005		

A significant F ratio would indicate that the slopes and/or intercepts differ beyond chance between the populations.

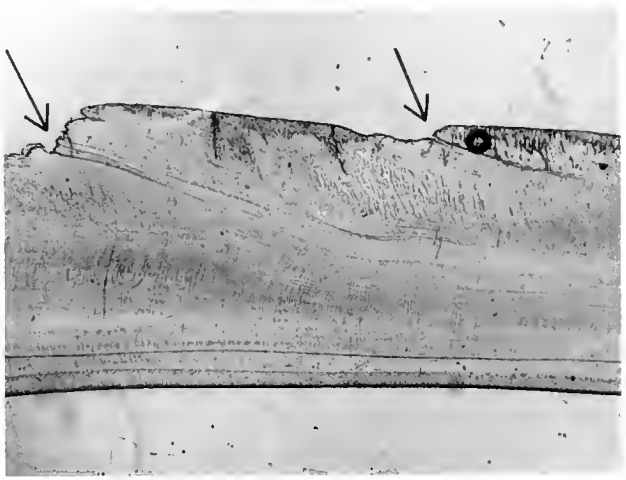

Figure 3. Photomicrograph of a portion of an acetate peel of the shell of *Crepidula fornicata*. The outer layer of the shell is at the top of the figure; arrows show two distinct growth lines.

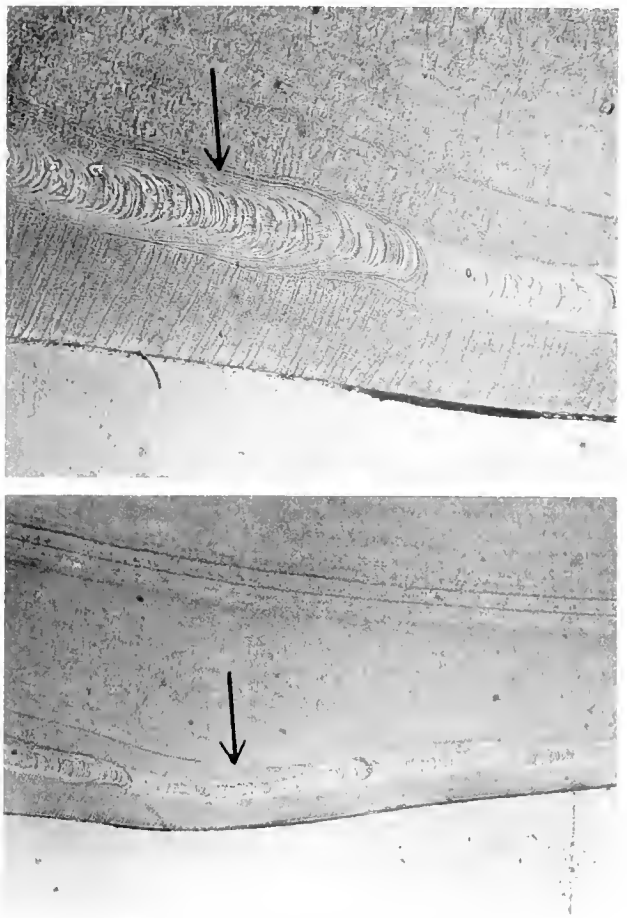

Figure 4. A. Microgrowth increments in the septum of *Crepidula fornicata*. The growing edge of the shell is to the right. B. Detail of above. Note variations in spacing of growth lines.

after metamorphosis. This determination is conservative because it assumes colonization by *C. fornicata* shortly after the crab's adult moult. In the Delaware Bay population sampled in this study, both adult male (prosoma width range, 18.1 to 23.7 cm) and adult female horseshoe crabs (23.2 to 33.0 cm), bore limpets exceeding 46 mm in length. There was no significant relationship between maximum limpet size and the prosoma width of the host crab (r^2 = 0.02, 30 df). This suggests that individuals of both sexes may live at least 8+ years beyond their terminal moult. By itself, our methodology cannot be used to indicate the maximum age of a crab. However, if we accept Shuster's (1950) estimate of 9–11 years to reach adult size, then the longevity of a horseshoe crab may be at least 17–19 years assuming the most conservative estimated age, 8 years, for the largest encrusting limpets.

In addition to providing insights into the age-structure of an adult horseshoe crab population, studies of their epifauna may have other value. For example, Caine (1986) differentiated between northern and southern populations of loggerhead sea turtles in the southeastern United States based on differences in fouling patterns. Many horseshoe crabs which spawn each spring on estuarine beaches from North Carolina to New York are dispersed on the middle Atlantic continental shelf during the cooler months (Botton and Ropes 1987b). It has not been established whether such crabs return to their natal estuaries for reproduction. A study of fouling organisms may be useful in determining whether discrete spawning populations of horseshoe crabs exist along the east coast of the United States, a question for which morphometric (Shuster 1979) and biochemical genetic (Saunders et al. 1986) data have provided somewhat different answers.

Inferences Concerning Longevity of Horseshoe Crabs

Shell length-shell weight relationships in slipper limpets were similar across populations and substrate type. Using age-length relationships derived from Walne (1956), and assuming that similar growth conditions prevailed in Delaware Bay, limpets of 5 to 6 cm length from horseshoe crab carapaces were estimated to be at least 8+ years old. This would imply that the crab host had not moulted for at least 8 years, since most limpets are sessile within a few months

ACKNOWLEDGMENTS

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RESOURCE ASSESSMENT OF PORTUNID CRABS IN ECUADOR

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ABSTRACT Five species of portunid crabs were identified in Ecuadorean coastal and estuarine waters. Relative abundance and distribution of *Callinectes* species were examined in the Guayas estuary. These appear to be sufficiently abundant to support the development of a small-scale fishery. Exploratory fishing for *C. toxotes* and *C. arcuatus* was conducted in the Guayas estuary from June through August 1987. Four gears were simultaneously fished: trotline, Chesapeake Bay trap, gillnet and liftnet. Approximate catch rates were estimated for each gear type based on measured CPUE's.

KEY WORDS: resource assessment, portunid crabs, swimming crabs, Ecuador, *Callinectes* crabs

INTRODUCTION

The portunid crabs, commonly referred to as the swimming crabs, are distinguished from the crawling crabs by the presence of a pair of flattened swimming dactyls on their last pair of pereiopods. Two species from the family Portunidae, the green crab, *Carcinus maenas* (Linnaeus) and the blue crab, *Callinectes sapidus* Rathbun have been extensively studied and literature abounds on their life histories and fisheries (Williams and Duke 1979). Very little is known about the ecology of the other 300 species of portunids, although they may play major roles in their ecosystems, as well as be potential unexploited resources for small or large scale fishing activities worldwide.

Williams (1974) and Garth and Stevenson (1966) cite the possible occurrence of eleven species of portunid crabs in Ecuadorean waters (disregarding occurrences in the Galapagos Islands): four from the genus *Portunus* Weber; one from the genus *Arenaeus* Dana; one from the genus *Cronius* Stimpson; two from the genus *Euphylax* Stimpson; and three species of the genus *Callinectes* Stimpson. In many cases, this proposed distribution is based on the presence of one individual animal in sampling records.

Based on previous field observations and conversations with commercial and artisanal fishermen in Ecuador, it appeared that swimming crabs were a non-utilized by-catch of the shrimp trawlers and artisanal fishermen. No information on the identification, life history, abundance or distribution of these crabs was available, nor had these crustaceans been considered in previous investigations for the development of alternative fisheries of underutilized species (FAO 1978, U.S. Dept. of Commerce 1982, Moran and Lopez 1984). Potential for the development of a fishery are great. All species of *Callinectes* swimming crabs are apt for human consumption and produce a highly acceptable food product if properly processed (Williams 1984, Norse and Fox-Norse 1979). The blue crab, *C. sapidus* is one of the most economically valuable crustaceans in the United States next to shrimp and lobster (Vondruska 1986).

This investigation examined the identification, relative abundance, distribution and catchability of the swimming crabs in Ecuador.

MATERIALS AND METHODS

Ecuador extends 950 kms along the western coast of the South American continent between the Latitudes of 1°00′ N to 3°20′ S. The country is bordered by Columbia to the north, Peru to the south and east, and the Pacific Ocean to the west. The configuration of the coastline is irregular, consisting of alternating bays and capes terminating in the Guayas Estuary and the Gulf of Guayaquil. This is the largest estuarine system on the western coast of South America. The area of the estuary and the Gulf of Guayaquil is estimated at 12,000 km^2 and extends 204 km from north to south (Borbor 1985). The ocean is defined as sub-tropical. The coast receives the influence of the Tropical Surface Water Body of the North Pacific with water temperatures exceeding 25°C and with a salt content below 33.5 ppt. Tides are semidiurnal with a period of 12.42 hours (Borbor 1985).

The climate is considered tropical and is divided into two distinct seasons. The wet season is characterized by heavy rainfall and extends from December through April; the dry season is cooler and includes the period from May through November.

The investigation of species identification was conducted during the dry season month of July 1986. The three

major estuarine systems along the Ecuadorean coast were sampled: Esmeraldas, Bahia de Caraquez and the Guayas Estuary (Figure 1).

Chesapeake Bay style crab traps were used to collect samples for the identification study (Van Engel 1982). The traps were constructed of locally available galvanized wire mesh, with a rectangular opening of 2.5 × 5.0 cm. During the resource study, a total of 41 trap hauls were made. Additional samples were obtained from local gillnet fishermen and commercial shrimp trawlers. Interviews with local fishermen were conducted to verify seasonal abundances of the species and approximate catch rates.

Samples for the abundance, distribution and catchability of *Callinectes* spp crabs were collected in the Guayas Estuary during the wet season (January) and the dry season (June–August) of 1987. Sites were located in three areas representing the upper, middle and lower estuary (Figure 1). The upper estuary is characterized by low salinities of 0–5 ppt, the middle estuary with intermediate salinities between 15–19 ppt, and the lower estuary with high salinities between 21–33 ppt.

Samples from the January 1987 period were collected using Chesapeake style crab traps. A smaller mesh version (2.5 × 2.5 cm) of this trap was constructed to retain juveniles. Samples from the July–August 1987 period were collected in four types of gear: crab trap, trotline, liftnet and gillnet. Fishing effort is expressed as gear-hour which represents one-unit of gear with a three hour soak divided by three. Defined units for each fishing gear are summarized in Table 1.

Bottom type, depth, salinity, soak time, bait, tidal stage, hour and catch were noted for each sampling period. Each crab was identified, sexed, measured and weighed. Width of the crab refers to the distance between the two longest cephalothorax spines. Crabs were identified according to Williams (1974) and Garth and Stevenson (1966). Maturity of females was determined by the configuration of the abdomen; maturity of males was determined by the looseness of their abdominal flap (Van Engel 1958).

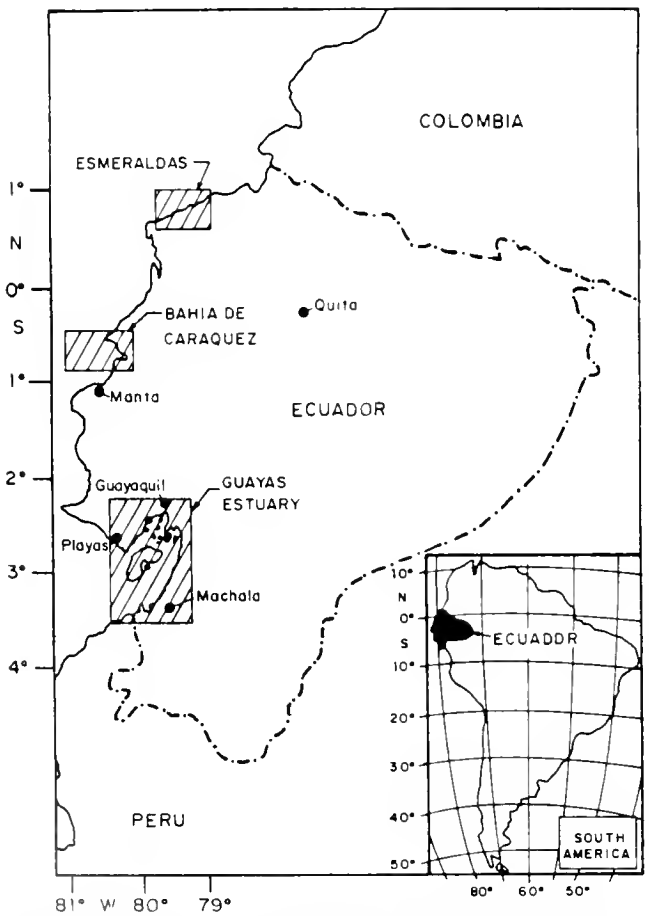

Figure 1. Map of Ecuador showing the three major estuarine systems sampled.

RESULTS AND DISCUSSION

Abundance and Distribution

The existence of five species of portunid crabs inhabiting the Ecuadorean coastal and estuarine waters was confirmed during these investigations. *Callinectes toxotes* Ordway and *Callinectes arcuatus* Ordway were captured in estuarine areas while *Euphylax robustus* A. Milne Edwards, *Portunus asper* (A. Milne Edwards) and *Cronius ruber* (Lamarck) were obtained from fishermen working in offshore areas. Preliminary data suggest that these latter three species are not of sufficient size or quantity to support a fishery in Ecuador. However, Hendrickx (1985) indicates that the large abundance of the genera *Portunus* and *Euphylax* in trawl nets in the Gulf of California may support a fishery in that area. In contrast, the data indicate the presence of a large unexploited *Callinectes* resource in Ecuadorean estuaries.

Callinectes toxotes was the largest of the swimming crabs found in the Guayas estuary and has been described as the largest species in the genus (Williams 1974). The largest specimen captured measured 22 cm in width, and weighed 660 g. The average width of *C. toxotes* captured was 14.9 cm ± 1.2 (female), 14.1 cm ± 2.9 (male) with average weights of 203 g ± 52.2 (female), 230.6 g ± 133.0 (male). *Callinectes arcuatus*, a smaller species, had mean carapace widths of 10.3 cm ± 1.9 (male), 8.2 ± 0.4 (female) and weights of 82.3 g ± 30.8 (male), 44.3 g ± 7.6 (female).

The data indicate that the species distribution found in the Guayas Estuary is similar to that described by Norse and Fox-Norse (1979) for sympatric populations of *Callinectes* and by Norse and Estevez (1977) along the Pacific coast of Columbia. *C. toxotes* dominated the less saline estuarine areas but was replaced by *C. arcuatus* in the higher salinity areas with some overlap in intermediate and high salinity areas. *C. toxotes* were found in the upper Guayas estuary during both sampling seasons. *C. arcuatus* and *C.*

TABLE 1.

Defined units of gear used in this study.

Gear	Defined Unit	Soak Time	CPUE
Trap	1 trap with mesh size of 2.5 × 5.0 cm.	3 h	Total catch divided by 3
Gillnet	30 × 1.5 m, 7.6 cm stretched mesh, leads every 1.5 m	3 h	Total catch divided by 3
Trotline	30 m of .6 cm line; bait every 1.5 m.	Fished every ½ h for 3 h.	Total catch divided by 3
Liftnet	1 square liftnet (64.8 cm with 1.2 cm) mesh webbing; bait in middle pocket.	Fished every ½ h for 3 h.	Total catch divided by 3

toxotes were found in the lower Guayas estuary in the dry season (no data is available for the wet season).

A differential species distribution was observed during the two sampling periods in the middle estuary (Figure 2). At the beginning of the wet season while bottom salinities were still relatively high (19 ppt), large populations of *C. arcuatus* were found. At the initiation of the dry season, salinities were lower (15–17 ppt) and the population consisted entirely of *C. toxotes*. No shift in species composition was seen in the upper estuary (0–5 ppt).

If *C. toxotes* and *C. arcuatus* follow a similar pattern of distribution as *C. sapidus* in the Chesapeake Bay, a differential distribution by sex and maturity can be expected. Mating would occur in the fresher areas of the estuary, with females later migrating to more saline areas to spawn, resulting in the dispersion of larvae into high salinity waters (Hail 1984).

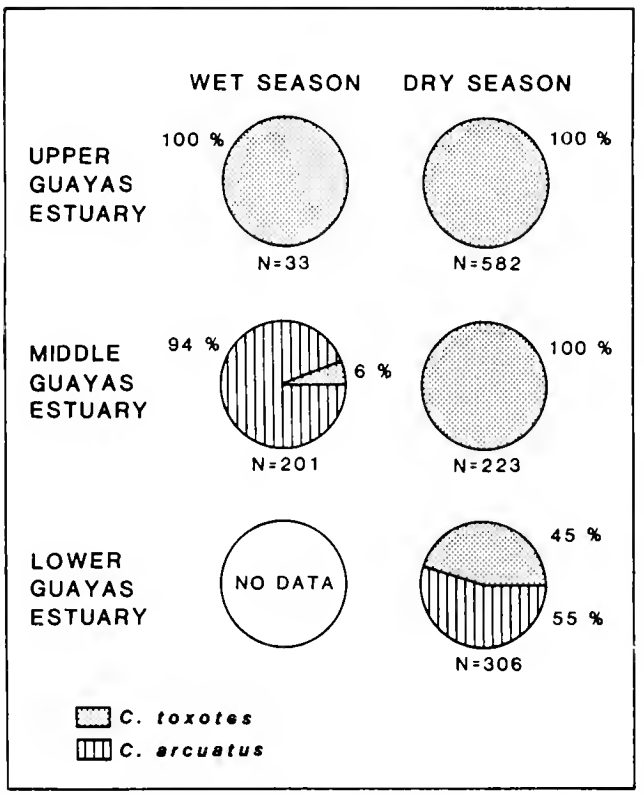

Figure 2. Relative distribution of *Callinectes* spp in the three areas of the Guayas estuary during the wet and dry seasons.

Assuming that the combination of sampling gears eliminated individual gear biases and catches represent the actual population structure, results indicate differential distribution of *C. toxotes* by sex and maturity in the three sites during the dry season sampling period (Figure 3). Data are not included from the wet season in the analysis due to the small sample size. Chi-square contingency table analysis was used to test population differences between the three sites (Sokal and Rohlf 1981). Results indicate significant differences in the distribution of mature males ($P < 0.001$), immature males ($P < 0.001$), mature females ($P < 0.001$) and immature females ($P < 0.05$). During the dry season, more mature males were observed in the lower estuary; more immature males were found in the middle estuary; more mature females were found in the upper estuary; and more immature females were found in the upper and lower estuary. These results do not indicate a similarity to the distribution described for *C. sapidus*, although data were restricted to a three month period and patterns may not be completely illustrated.

The majority of the *C. arcuatus* captured were males. Principally mature males were found in the middle Guayas estuary, and mature and immature males were found in the lower estuary (Figure 3). Very few females were captured, which suggests their absence from the estuarine areas sampled. Dittel et al. (1984) in their investigations on *C. arcuatus* in Costa Rica, captured mostly females, but their sampling was conducted by trawling offshore in the Gulf of Nicoya. The Gulf of Guayaquil was not sampled in this study, but literature supports the theory that *C. arcuatus* and *C. toxotes* may form large breeding populations in coastal waters throughout the year (Rosales 1976) and that the estuarine phase of the life cycle is a growth phase as suggested for *Callinectes latimanus* in Ghana (Kwie 1978). Paul (1982a and b) found that in Mexico, the female *C.*

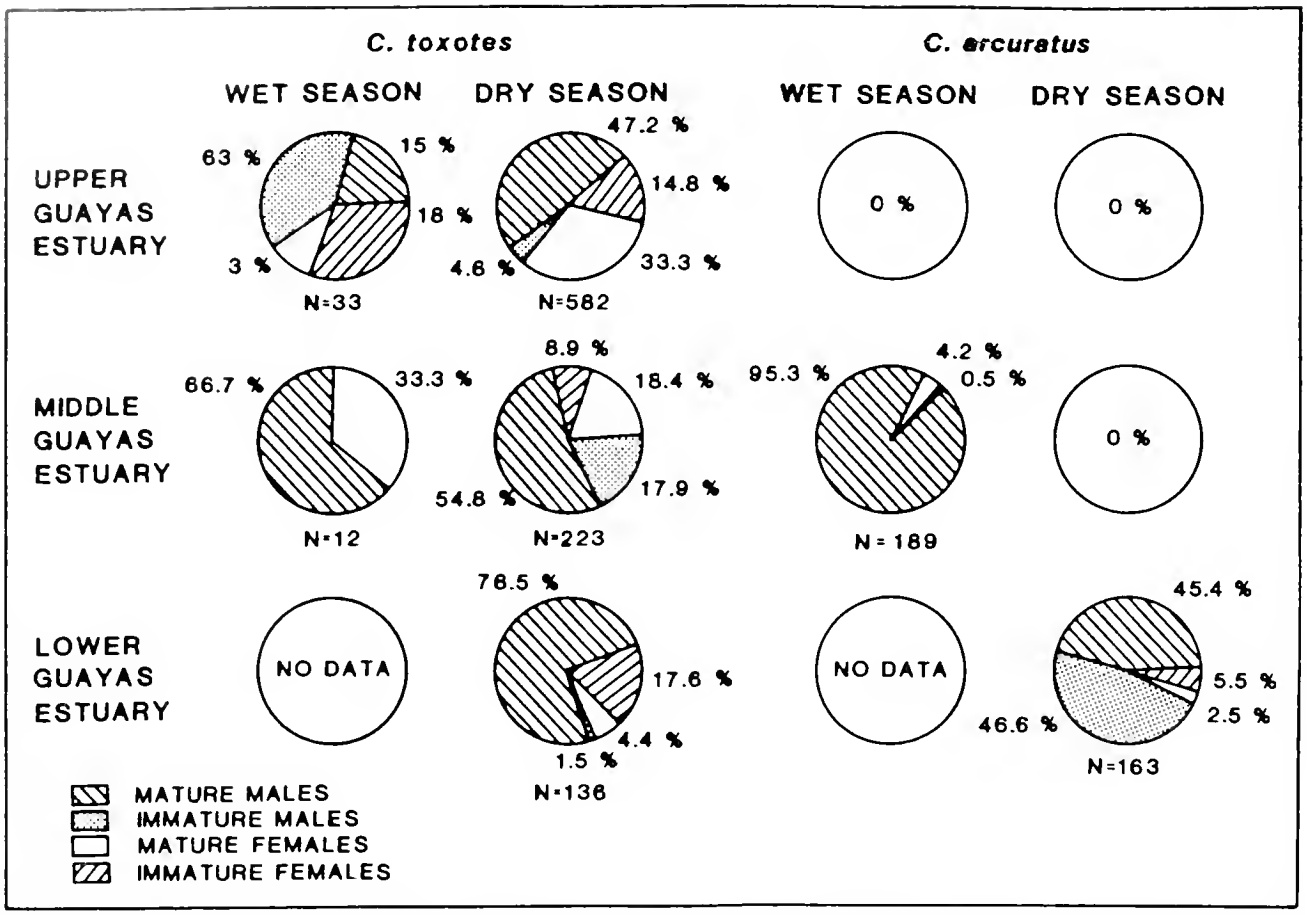

Figure 3. Relative proportions of *Callinectes* spp crabs based on sex and maturity in three areas of the Guayas estuary during the wet and dry seasons.

arcuatus continue their migration out of the estuary and continue spawning out on the continental shelf. Ecuadorean shrimp trawlermen reported large seasonal catches of *C. arcuatus* in the Gulf of Guayaquil.

General aspects of crab size and weight are of considerable interest to both fishermen and ecologists. Of interest to fisheries managers is size/age at sexual maturity. Age is difficult to determine for decapods in general, but size (width/length) can be used to set some limits for sexual maturity although these can vary in different geographical locations. Sexual maturity is an important parameter because it may indicate the start of reproductive activity although Cobb and Caddy (in press) make a distinction between functional and physiological maturity in *Homarus americanus*. Through management regulation of gear, fishing season or location, a certain percentage of the immature population can be protected and allowed to contribute to future recruitment before becoming vulnerable to fishing gears.

Results of size at sexual maturity in crabs captured in this investigation indicate that immature male *C. toxotes* range from 2.1 to 17.5 cm in width. The 50% mature/immature range is between 10.6 and 11.0 cm. Immature female *C. toxotes* range from 1.1 to 17.0 cm in width with the 50% mature/immature size between 13.6 and 14.0 cm (Figure 4). Immature male *C. arcuatus* ranged from 5.1 to 12.5 cm with the 50% mature/immature size between 8.6 and 9.5 cm. Immature female *C. arcuatus* range from 4.6 to 8.0 cm with 50% mature/immature size range between 7.6 to 8.0 cm (Note: small sample size for females) (Figure 4).

Catchability

The blue crab in the United States is subject to diverse types of fishing gear (Haefner 1985). Gears can range from a simple baited hand line to the 50 kg crab dredge used in the winter months in the Chesapeake Bay. Only a few gears have proven to be economically practical on a commercial basis (Sholar 1979): crab traps (80%), trotlines (10%), and dredges (10%). In Ecuador, there are technological, social, cultural and environmental factors that must be considered in the selection of the appropriate harvesting gear. The most appropriate harvesting gear should be a compromise between these factors, as well as performance data for each gear type in the Guayas estuary.

Gear performance was measured by the catch per unit

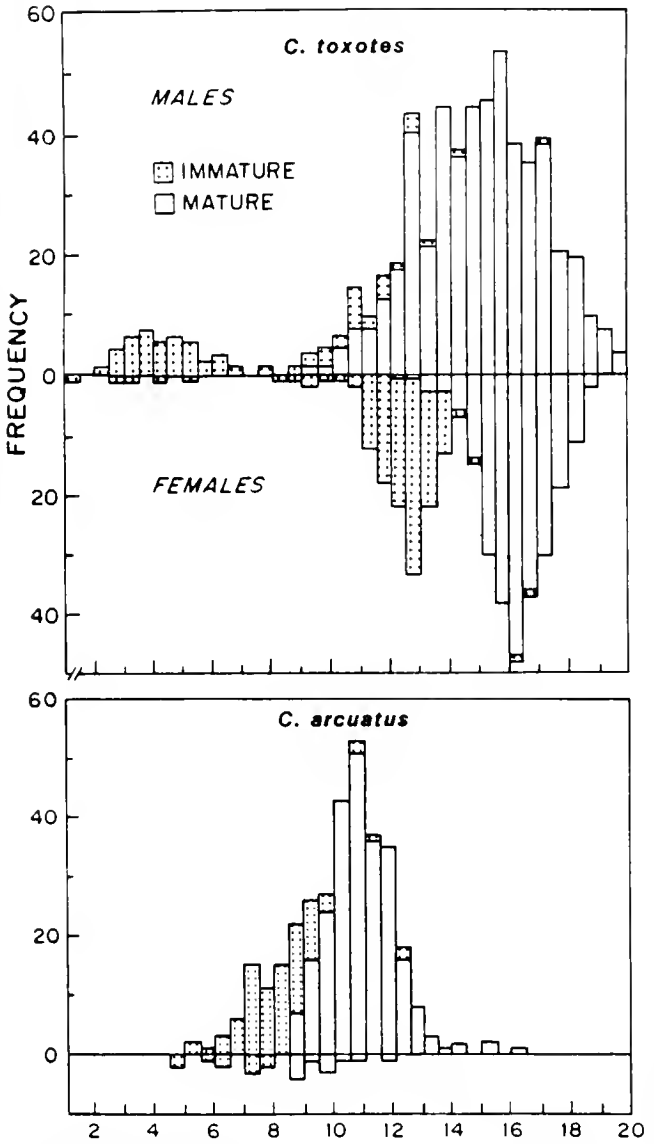

Figure 4. Width frequency of mature and immature *Callinectes* crabs in the Guayas estuary.

effort (CPUE) which was defined in this study to be the number of crabs caught during a one hour period by one defined gear unit. Average CPUE for each gear was obtained by taking the mean for all replicates used in each site (Table 2).

Gears performed differently in each site and in relation to each other. Unlike the results obtained by Bishop et al. (1984), no similar patterns among gears were observed between sites. The gillnet produced the highest CPUE in the upper estuary while liftnets produced the highest CPUE in the middle and lower estuary. These differences might be attributed to behavioral characteristics of the crabs (baited vs. non-baited gears) or different environmental parameters, such as strong currents, affecting gear performance.

Since variability in CPUE between replicates and trials was great, one-way ANOVA analysis showed no significant differences in CPUE in gear type in the upper and lower estuary. However, liftnets produced a significantly higher CPUE than either gillnets or traps in the middle estuary ($P < 0.001$).

The width frequencies (sizes) of the crabs captured per gear type over the sampling period were analyzed with the Kruskal-Wallis non-parametric test. Significant differences were seen in the upper estuary ($P < 0.005$) and the middle estuary ($P < 0.005$). In both sites, smaller crabs in the catch of the liftnet were present. This probably accounts for the higher CPUE of the liftnets in the middle estuary due to the great number of small crabs caught by this gear. All other gears did not retain the smaller animals. In the lower estuary there were no significant differences between the width frequency of the total catch and the gear involved, although the number of crabs captured was much lower than other sites.

To examine the possibility of sex or maturity influencing the selectivity of the gears, the average CPUE of each population sector was analyzed by gear type using a one-way ANOVA. No significant differences between gears were found in the upper or lower estuary for the capture of *C. toxotes*. However in the middle estuary, a significant difference was found in the CPUE of immature males in liftnets which agrees with the results pertaining to the retention of smaller animals by this gear and the availability of these size crabs in this site. Liftnets additionally demonstrated selectivity for immature *C. arcuatus* in the lower estuary.

In summary, gear type, using the unit-effort defined in this study, did not affect the catch of mature crabs. Liftnets produced a higher CPUE because of the inclusion of the smaller immature crabs which would not be marketable.

TABLE 2.

Average catch per unit effort (CPUE) expressed in number of mature crabs captured by gear type and site for the dry season.

	Gillnet	Traps	Trotline	Liftnet
Upper Guayas Estuary	1.03 (8)	0.56 (30)	0.86 (10)	0.53 (25)
Middle Guayas Estuary	0.23 (8)	0.66 (29)	0.91 (8)	1.40 (20)
Lower Guayas Estuary	0.36 (12)	0.47 (35)	0.08 (4)	0.48 (15)
Average CPUE	0.52 ± .78 (28)	0.56 ± .52 (94)	0.74 ± .94 (22)	0 83 ± .92 (60)

Number of replicates is indicated in the parenthesis.
± = standard deviation.

TABLE 3.

Estimated catches of *Callinectes* spp crabs based on CPUE data and assumption of constant catch rate over time.

Artisanal Level				Small-Scale Commercial Level			
Gear	Units	Soak Time (hrs)	Catch	Gear	Units	Soak Time (hrs)	Catch
Trap	10	24	134	Trap	100	24	1350
Lift Net	10	8	58	Lift Net	100	8	584
Trotline	200 m	8	43	Trotline	1600 m	8	376
Gillnet	200 m	12	43	Gillnet	1600 m	12	374

Due to the mesh size available for trap construction, small animals were not retained. Gillnets did not retain juveniles for unknown reasons; and when fishing trotlines, small crabs were usually not spotted while retreiving gear and dropped off or fell through the meshes of the fishing basket.

The CPUE of both trotline and liftnets can be dramatically affected by soak time; if fished at shorter intervals, the CPUE can be expected to increase. The CPUE for gillnets and traps are subject to saturation or interaction effects with increasing soak time so CPUE may actually decline with increasing soak time (Ricker 1975).

If the assumptions are made that the catch rate is constant during the entire fishing time and effects of gear saturation and species interaction are minimal, CPUE can be extrapolated into expected daily catch for an artisanal fisherman working from a non-motorized vessel such as a canoe, and for a small-scale commercial fisherman with a motorized vessel less than 6 m in length (Table 3).

It is difficult to definitely ascertain the resource potential of *Callinectes* spp from this study, although the results do offer some insight. Crabs were captured in all of the areas sampled although variability in the catch rates was due in large part to the exploratory nature of this investigation. From the data obtained thus far, we believe that the *Callinectes* spp crab resource is sufficient to sustain an artisanal based fishery. However, it is recommended that more detailed investigations be conducted before any large scale commercial level fishery be established for this resource.

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MUD CRAB (CRUSTACEA: BRACHYURA: XANTHIDAE) SUBSTRATE PREFERENCE AND ACTIVITY[1]

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ABSTRACT Substrate choice of xanthid mud crab species (*Neopanope sayi*, *Panopeus herbstii*, and *Eurypanopeus depressus*) was investigated for the purpose of defining appropriate substrates for field growout of cultured bivalves under risk of predation from mud crabs. Crabs of all three species preferred burial in broken oyster shell most, and sand least, when offered shell, mud, small gravel, large gravel, and sand in binary substrate choice trials of 22 h duration. *Neopanope sayi* was the most active species (changed between substrates most often), based on short-duration observations of crab location and activity taken at different stages of a photoperiod which incorporated dawn and dusk periods. Increased nocturnal activity changed the daylight substrate preferences exhibited by *N. sayi* and *E. depressus*. Substrate preference experiments should be conducted under reasonable approximation to natural photoperiod, be of sufficient duration to elicit other than initial substrate choice, and involve repeated observations on animal behavior.

KEY WORDS: substrate preference, activity, *Neopanope*, *Panopeus*, *Eurypanopeus*

INTRODUCTION

Relatively little is known concerning the substrate preferences of brachyuran crab species. Distributional data identify particular substrates in which certain species are found, but do not indicate whether these are preferred substrates. Non-preferred substrates are typically inferred from sampling in areas where few or no crabs are present. Several factors, such as, food availability, predator presence, reproductive or molt condition, and dominant environmental factors (e.g. temperature, salinity and near-bed tidal currents) may restrict crabs to specific substrates.

Based on distributional data, the xanthid mud crabs, *Neopanope sayi* (Smith), *Eurypanopeus depressus* (Smith), and *Panopeus herbstii* (H. Milne-Edwards), are most abundant on oyster beds (McDermott and Flower 1953), mud bottoms (Williams 1984), or oyster shell bottoms (WAPORA, Inc. 1981, Arnold 1984, Williams 1984). *Panopeus herbstii* is also found in burrows along the edges of higher marshes (Williams 1984). On Long Island, New York, *N. sayi* abundance increased as gravel grain size increased in experimental field plantings of cultured juvenile bivalves (Flagg and Malouf 1983).

The work described herein was one of several studies designed to investigate techniques for altering crab behavior in ways that reduce the impact of crab predation on juvenile hard clams, *Mercenaria mercenaria* (L.). (Details available from the second author.) One technique to artificially enhance juvenile hard clam survival involves using crushed stone or shell aggregate to protect young clams from predation by large crab species, such as portunid crabs (Menzel et al. 1976, Castagna and Kraeuter 1977, Kraeuter and Castagna 1977, Flagg and Malouf 1983). This technique may not be suitable, however, in situations where small crab species, such as xanthid crabs, are abundant. Mud crabs may be protected from their natural predators in such substrates.

The present study had two purposes:

1. Identify the order of substrate preference for three co-occuring xanthid mud crab species (*Neopanope sayi*, *Eurypanopeus depressus*, and *Panopeus herbstii*) in several natural and prepared substrates, particularly these crab's least preferred substrates for later use in predation experiments; and
2. Determine whether mud crab substrate preference and activity level are affected by light regime.

MATERIALS AND METHODS

Substrates and Experimental Animals

Small gravel (bluestone, less than 17.0 mm diameter), large gravel (bluestone, greater than 30.0 mm diameter), broken oyster shell (each piece approximately 40 × 60 mm), and beach sand (sieved through a 1000 μm, no. 18 mesh) were washed in fresh water, allowed to air dry, and stored in uncovered bins. Mud (sieved through a 250 μm, no. 60 mesh) was stored in a 5°C cold room to minimize growth in any residual plant and animal populations.

Male *Neopanope sayi* (20.0–25.85 mm carapace width, CW, measured to the nearest 0.05 mm, including spines), male *Eurypanopeus depressus* (20.0–28.05 mm CW) and female *Panopeus herbstii* (20.2–27.9 mm CW) were used

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for determining species-specific substrate preferences. Insufficient numbers of appropriately-sized male *P. herbstii* were encountered during field collections, thus trials with this species were conducted exclusively with female crabs. No female *P. herbstii* in berried condition were used, however, in an effort to reduce the potential for sex-biased substrate preference. Mud crabs of all three species were collected from intertidal and shallow subtidal locations in Flax Pond, a tidal salt-marsh in Old Field, New York.

Systematic sampling (60 min searches) of three intertidal habitats at Flax Pond (a gravel beach adjacent to an inlet channel; a mud/sand beach adjacent to a *Spartina alterniflora* (Loisel) marsh; and in burrows among *S. alterniflora* root masses) was used to assess species-specific distribution in the field, Subsequent to these sampling efforts, *N. sayi* was collected in traps (0.61 m × 0.61 m × 0.25 m) baited with crushed mussels, *Mytilus edulis* L., and placed in water approximately 1 m deep. *Eurypanopeus depressus* and *P. herbstii* continued to be collected from burrows in and around *S. alterniflora* plants.

Prior to use in trials, newly-captured crabs were maintained communally (for less than one month) in holding tanks provided with running seawater (20.0–24.5°C; 26–30‰), but lacking substrates. Tanks were illuminated by flourescent and indirect natural light. Crabs were fed ad libitum, three times a week, on the flesh of crushed clams and mussels. Intermolt crabs, having both claws and more than six walking legs intact, were selected from this stock of animals. Each crab was used in only one substrate preference trial.

Substrate Preference Experiment

Five substrates (mud, sand, small gravel, large gravel, and broken oyster shell) were presented in binary combination, creating ten substrate combinations which were replicated three times. Trials were conducted in opaque plastic containers (0.025 m^2 basal area, 0.25 m H × 0.17 m base diameter). Although relatively small, these containers held sufficient amounts of each test substrate to permit 20–30 mm CW crabs to burrow in a selected substrate, and ensured contact with both substrates during active periods. Twenty-four hours before each trial, 30–50 mm of the two chosen substrates and seawater (to a total depth of 0.18 m) were added to each container. An aquarium air pump provided continuous aeration to each bucket while the substrates settled overnight.

The substrate preference experiment was conducted in an experimental facility developed by the second author at the Marine Sciences Research Center, State University of New York, Stony Brook, New York. Mud crabs were acclimated to the system for two weeks prior to use in trials. The aquarium room lighting system comprised 14, 40 watt, fluorescent lights (having a light spectrum similar to natural daylight) connected to a custom-built dimming unit. Daily dawn and dusk crepuscular periods were thus provided in which the illumination level progressively changed over a 75 min period. The onset of each crepuscular period was adjusted daily, using a microprocessor-based timing unit, to approximate the seasonal progression of natural sunrise and sunset. Night observations were made under illumination provided by four safelight lamps having 40 W incandescent bulbs and red safelight filters. These lamps emitted light of wavelengths greater than 600 nm, to which brachyuran crabs have low sensitivity (Cronin 1986).

Prior to use in a trial, crabs were fed to satiation on clam or mussel flesh (over a 4 h period), then starved for 24 h to standardize hunger level (sensu Elner and Hughes 1978). Male *Neopanope sayi*, male *Eurypanopeus depressus*, and female *Panopeus herbstii* were tested in succession in each substrate combination.

To initiate a trial, a crab was placed into a section of PVC pipe, the base of which was centered on the interface of the two substrates. After a 2 min acclimation period, the pipe was slowly removed allowing the crab to move over the two substrates. Six or nine trials were run concurrently, with the initiation time of individual trials sequenced such that subsequent observations could be taken at equivalent times following initial release. Each trial lasted 22 h, with the first trial of each set commencing at 12:00 and terminating at 10:00 on the following day.

During each observation period, the location and posture of each crab was recorded, as was the time at which any change between substrates occurred. A crab was determined to be "on the interface" when it was in contact with both substrates simultaneously. Observations were taken initially (5 min after the crab was released from the pipe), during daylight of the first day, at dusk, during night, at dawn, and during daylight of the second day (Table 1).

The Kruskal-Wallis distribution-free one-way analysis of variance (Hollander and Wolfe 1973) was used to test for differences in the amount of time crabs spent on each substrate, and on the interface of each substrate combination, in each of the different light regimes. Multiple comparisons were performed by a Kruskal-Wallis rank sums test (Hollander and Wolfe 1973) to determine where significant differences existed. A conservative variation of this procedure was used that allowed for unequal and large sample sizes. All statistical tests were evaluated at a significance level of 0.05. Analyses were performed separately for each crab species.

RESULTS AND DISCUSSION

Substrate Preference and Activity Level

In each laboratory experiment, xanthid mud crabs exhibited preferences for substrates that were characterized by complex topography. The general preference was the same for all three species; shell was most preferred and sand was least preferred, but the details of substrate preference differed. Overall order of substrate preference for *Neopanope*

TABLE 1.

Number (N) and duration (min) of observations made on the substrate choices and activity levels of three mud crab species: *Neopanope sayi*, *Eurypanopeus depressus*, and *Panopeus herbstii*.

		N. sayi		*E. depressus, P. herbstii*	
Period	**Time of Day**	**N**	**min**	**N**	**min**
1. Initial	5 min from crab entry onto test substrates–65 min	2	2	1	5
2. Day 1	14:30–16:00	2	2	1	5
3. Dusk	10 min from start of 75 min dusk period–60 min	2	2	2	2
4. Night	11:00–00:30, 02:30–04:00	4	2	2	5
5. Dawn	10 min from start of 75 min dawn period–60 min	2	2	2	2
6. Day 2	09.00–10:00	2	2	1	5

sayi (disregarding light regime as a factor) ranked from most to least preferred substrate, was: shell, small gravel, large gravel, mud, and sand (Table 2). *Eurypanopeus depressus* exhibited a similar order of substrate preference (Table 2), except that large gravel was preferred over small gravel. The order of substrate preference for *Panopeus herbstii* was somewhat different in that large gravel was preferred only over sand, while mud was preferred over both of these substrates (Table 2).

These differences in substrate preference may be related to the specific morphology and physiology of each species. *Neopanope sayi* and *Eurypanopeus depressus* are very similar morphologically and in maximum size (Lawton 1989). McDonald (1982) noted that in addition to growing twice as large, *Panopeus herbstii* has a greater carapace height to carapace width ratio than *E. depressus;* this prevents *P. herbstii* from entering the spaces between oysters, and instead this species occupies grottoes and depressions at the mud/oyster reef interface. *Eurypanopeus depressus*, however, is able to find refuge in the narrow spaces between living oysters on oyster reefs (McDonald 1982).

Substrate preference changed over the duration of the experiment for each mud crab species (Figure 1). This change occurred between preference for a particular substrate and no preference in every case except two (*Panopeus herbstii;* mud vs. small gravel, and sand vs. small gravel). For example, in the combination of sand and shell, shell was always preferred, or there was no preference shown; sand was never preferred over shell (Figure 1). The current study considered both substrates and the interface between them as potential substrate choices for the crabs. Crabs may make no substrate choice either by spending equal portions of time on both substrates, or by spending a large portion of time on the interface.

This laboratory data is consistent with field distributional data, including that obtained in the present study (Table 3, personal observations), which indicates that xanthid mud crabs are found in a variety of substrates which offer some type of cover. Oyster reefs and bottoms littered with oyster shells and live oysters provide a good habitat for *Panopeus herbstii* (McDermott and Flower 1953, May 1974, McDonald 1982, Reames and Williams 1983, Walker and Tenore 1984), and *Eurypanopeus depressus* (Ryan 1956, May 1974). May (1974) stated, "There were more crabs [*P. herbstii*] on reefs which had boxes (empty joined bivalve shells) and single shells indicating strong dependence on habitat provided by shells." Ryan (1956), however, also found *P. herbstii* and *Neopanope sayi* on soft mud bottoms which had few oyster shells. *Neopanope sayi* may be found on soft vegetated bottoms (Wass 1955), while *P. herbstii* often occurs under rocks and between stones on jetties (Hazlett 1979), in

TABLE 2.

Overall substrate preference of three mud crab species, family Xanthidae. Substrate ranking determined as the number of times a particular substrate was preferred in each of 10 substrate combinations.

	Neopanope sayi		*Eurypanopeus depressus*		*Panopeus herbstii*	
Order	**Substrate**	**Rank**	**Substrate**	**Rank**	**Substrate**	**Rank**
Most	Shell	3*	Shell	4	Shell	4
•	Sm. Gravel	3*	Lg. Gravel	2	Sm. Gravel	2*
•	Lg. Gravel	2	Sm Gravel	1*	Mud	2*
•	Mud	1	Mud	1*	Lg. Gravel	1
Least	Sand	0	Sand	0	Sand	0

* = In the case of tied ranks, the trial comparing the two tied substrates was used to determine preference.

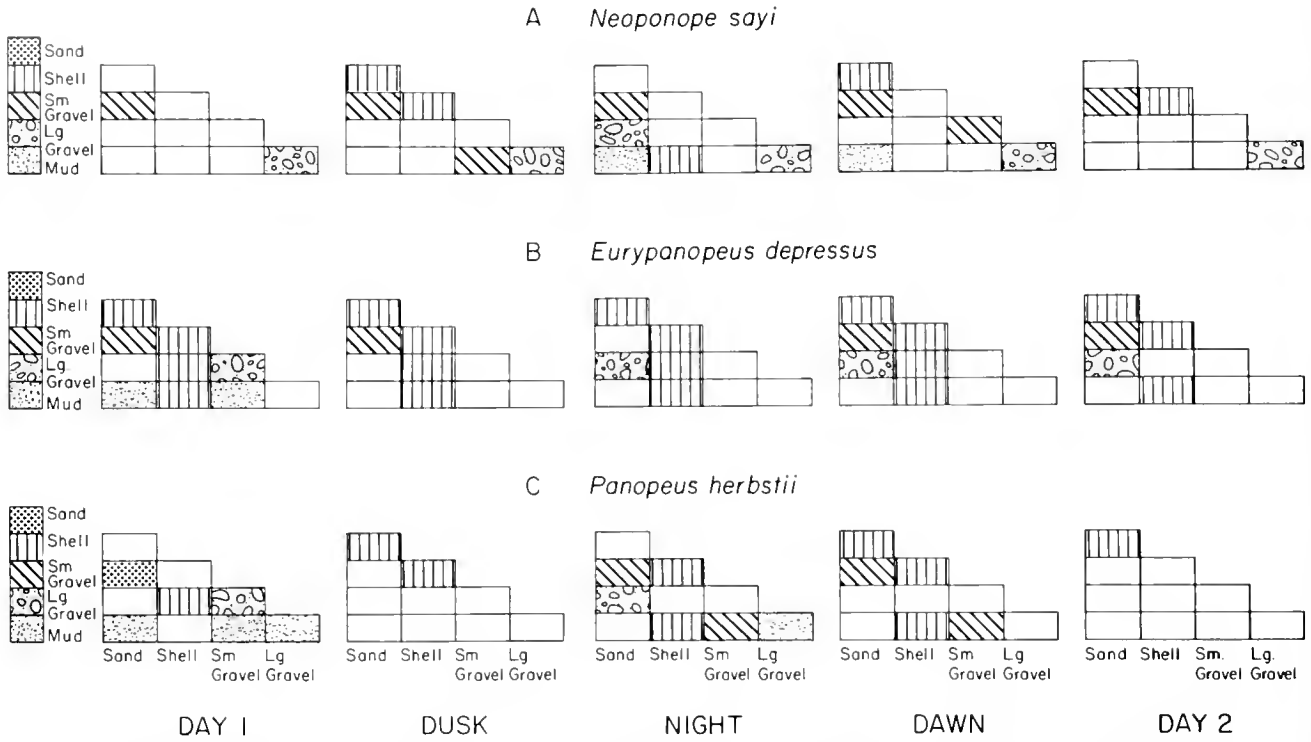

Figure 1. Preferred substrate of each binary substrate combination presented to, (A) *Neopanope sayi*, (B) *Eurypanopeus depressus*, and (C) *Panopeus herbstii* during each light regime of the experiment. The preferred substrate of each substrate combination is depicted graphically in the corresponding cell; blank cells indicate that no preference was shown in that substrate combination.

burrows along mud banks, and among roots of marsh grass (Reames and Williams 1983). Walker and Tenore (1984), in a study on the distribution and production of hard clams in Wassaw Sound, Georgia, found no *P. herbstii* or other mud crab species in sandy mud areas.

The strong association of *Eurypanopeus depressus* with *Spartina alterniflora* plants at the Flax Pond site (Table 3), and omission of vegetated substrates in the substrate preference experiments requires explanation. An objective of this study was the identification of substrates for use in hard clam mariculture for which crabs exhibit low preference and in which they may be exposed to their natural predators. This consideration preempted the inclusion of *Spartina* as a test substrate. It should be noted, however, that planting seed clams in close proximity to *Spartina* banks may increase the risk of losses due to mud crab predation.

Crab activity was analyzed by counting the number of times individual crabs of each species crossed between the substrates during each observation period. Using this measure of activity, *Neopanope sayi* was clearly the most active of the three mud crab species during all five light regimes. The number of changes between substrates $\cdot$ crab^{-1} $\cdot$ min^{-1} for *N. sayi* ranged from 0.14 to 0.25 (Fig. 2A), whereas values of this measure of activity were never greater than 0.05 for *Eurypanopeus depressus* and *Panopeus herbstii* (Fig. 2B–C). *Eurypanopeus depressus* and *N. sayi* showed increased activity as indicated by a greater number of changes between substrates $\cdot$ crab^{-1} $\cdot$ min^{-1} at night and/or dusk (less than full illumination) than during day 1 or day 2 (full illumination; Figure 2).

There was some evidence that increased activity (Figure 2) led to changes in substrate preference (Figure 1) during dusk observations on *Neopanope sayi* and night observations on *Eurypanopeus depressus*, however, these effects were not dramatic. Alternatively, changes in substrate pref-

TABLE 3.

Distribution of three mud crab species, family Xanthidae, collected from three distinct intertidal habitats at Flax Pond, Old Field, New York, June 25, 1986. Indicated is carapace width (CW) range and sample size (N) for each species, subdivided by sex (males = 1; females = 0).

Location	Species	Sex	CW Range (mm)	N
Gravel	*N. sayi*	1	9.7–24.8	21
		0	9.4–18.2	4
Mud/Sand	*N. sayi*	1	20.9	1
	E. depressus	1	23.4–24.7	3
		0	13.9–16.4	2
	P. herbstii	0	23.5–25.3	2
Spartina/Mud	*E. depressus*	1	8.4–28.0	34
		0	8.1–21.5	33
	P. herbstii	1	17.6–33.9	7
		0	17.3–28.1	6

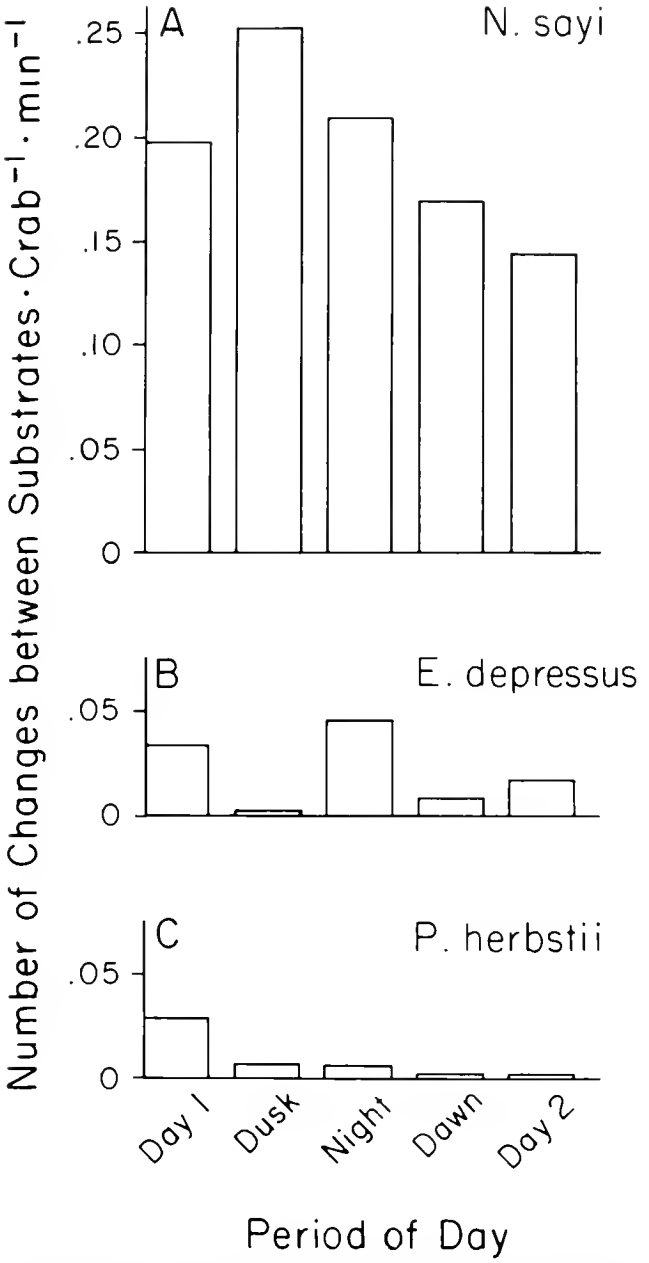

Figure 2. Mud crab activity represented as the number of changes between substrates · crab^{-1} · min^{-1} for, (A) *Neopanope sayi*, (B) *Eurypanopeus depressus*, and (C) *Panopeus herbstii*, during each light regime of the experiment.

erence of *Panopeus herbstii* between day 1 and night observations were apparently correlated with decreased activity. Diel activity patterns have been documented in several crustacean species (Cobb 1981, Lipcius and Herrnkind 1982, Lawton 1987, Rebach 1987) making repeated observations especially important when determining the substrate preferences of crab species.

Implications

The procedures used in this study were adopted to simulate natural conditions as closely as possible, while minimizing artifacts associated with conducting substrate preference experiments in a laboratory setting. The only comparable study is that by Arnold (1984) who examined substrate preferences of blue crabs, *Callinectes sapidus* Rathbun, using paired-substrate trials. Natural illumination was provided on a 14 h light: 10 h dark schedule, with fluorescent lights used to enhance daytime illumination. Trials were initiated by "gently placing the animal over the line of intersection of the sediments." A 15 min acclimation period was allowed before observations were taken at 5 min intervals for 50 min. No observations were taken at night. In the current study, observations on substrate preference were taken over a 22 h period covering all light regimes. When a trial was initiated, each crab was held in a section of pipe at the interface of the two test substrates to ensure that the crab experienced both substrates prior to being released. By holding crabs at the interface of the two substrates it was anticipated that any potential for a fright-flight response upon release into the experimental situation would be diminished.

Other behavior studies have used fluorescent lighting set at a specific light:dark cycle that was not adjusted daily and/or did not provide crepuscular periods (Whetstone and Eversole 1981, Arnold 1984, Herrnkind and Butler 1986, Lipcius and Hines 1986). In research on nephropid and palinurid lobster shelter occupancy (Cobb 1971, Cobb 1981, Pottle and Elner 1982, Richards and Cobb 1986), observations on lobster activity and location have typically been made only at dusk and/or at dawn. A more recent study (Lawton 1987) revealed a complex pattern of shelter use by juvenile lobsters, *Homarus americanus* H. Milne Edwards, when analysis of a video record was used to determine the pattern of lobster activity during various light regimes.

Observations on *Panopeus herbstii* during day 1 showed the greatest preference for mud, followed by an equal preference for sand, large gravel and shell. Small gravel was not preferred in any substrate combination during this light regime. Observations during dusk, however, indicated shell as the only substrate where a preference was shown. Not until night was there an order of substrate preference exhibited that was similar to the overall substrate preference of this species (Figure 1C). Had the lighting system not followed the natural photoperiod so closely, or had the length of each trial been shorter, the importance of shell as the most preferred substrate, and sand as the least preferred substrate, may have been overlooked.

Neopanope sayi was the most active of the three co-occurring mud crab species, as indicated by the high number of changes between substrates (Figure 2), and the most abundant mud crab in the areas sampled for this study. Such evidence suggests *N. sayi* may be the most significant mud crab species preying upon juvenile hard clams in Long Island waters. Clearly, substrate preference will be affected by prey distribution and diel foraging activity. Information presented herein which indicated that mud crabs exhibit a

low preference for sand when compared to gravel substrates, was used in a subsequent study which examined the effect of substrate type and predatory risk on *Neopanope sayi* predation of juvenile *Mercenaria mercenaria* (Day 1987).

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TRAP MESH SELECTIVITY IN RELATION TO THE LEGAL SIZE REGULATION FOR PRAWN (*PANDALUS PLATYCEROS*) IN BRITISH COLUMBIA

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ABSTRACT Experimental trap fishing for prawns, *Pandalus platyceros* Brandt, in a British Columbia fjord revealed that mesh size variations can permit escapement of sublegal-sized prawns while not decreasing catches of legal-sized prawns. We provide recommendations on prawn savings gear for an industry that has recently acquired a legal prawn size restriction.

KEY WORDS: prawn, *Pandalus*, trap selectivity, mesh size

INTRODUCTION

Three important functions of size limits in invertebrate fisheries are:

1. Preventing growth overfishing, which Miller (1976) cites as the rationale for the size limit on snow crab (*Chionoecetes opilio* Fabricius) in eastern Canada,
2. Protecting part of a population for reproduction prior to harvest, as seen in the northeast Pacific Dungeness crab fishery (*Cancer magister* Dana) (Miller 1976), and
3. Protecting adults who aid recruitment by providing nursery shelter for conspecific juveniles, as for the red sea urchin (*Strongylocentrotus franciscanus* (Agassiz)) in British Columbia (Breen 1984).

Boutillier (1984) recommended a minimum size limit of 30 mm carapace length (CL), *sensu* Butler (1964), to prevent growth overfishing in the British Columbia prawn (*Pandalus platyceros* Brandt) trap fishery. Two problems were identified with this regulation:

1. Variability of growth rates between areas, and
2. Allowing escapement of undersized prawns.

Boutillier (1985a) discusses variable growth rates and we report here on escapement of undersized prawns. The British Columbia prawn industry currently operates without gear restrictions (Boutillier 1985b). We wish to document how to minimize catches of sublegal prawns using savings gear, while maintaining catch rates of legal prawns.

MATERIALS AND METHODS

The mesh size experiment was completed in Alberni Inlet (Figure 1) during the summer of 1985. Alberni Inlet is a deep (>300 m), steep-walled fjord on the west coast of Vancouver Island, and has been one of the major commerical prawn producing areas in British Columbia. The Spencer Creek location was chosen from areas with potential commercial quantities of *P. platyceros* determined by a series of pre-study sets. Alberni Inlet was closed to commercial harvesting throughout the study period.

The five trap type characteristics, three "Pardiac" nylon mesh types and two "wire mesh" types, are listed in Table 1. Traps were set for 24 h, 48 h and 72 h soak times. Eight traps of each type were attached in random sequence, 10 m apart on a groundline deployed at 80 to 100 m depth at the Spencer Creek site. Five sets for each soak period were made in a random series. Each trap was baited with a 100 g can of sardines packed in edible oil. Baits were used only once. Captured prawns were counted, measured for carapace length and removed from the study site. To estimate the weight of prawns caught, we used Butler's (1964) conversion formula:

$$\log \text{total } P.\ platyceros \text{ weight} = 2.93148 \log \text{carapace length} - 3.07787.$$

Catch weights were used as they are the basis by which fishermen would evaluate different trap types.

For the mesh experiment, analyses of variance for repeated measure models with equal or unequal cell size were done using programs from the BMDP Biomedical Computer Program Package. Data were analysed by standardized set in which the catch of the 8 traps of each type were combined. The catch was standardized by set to compensate for a single lost trap in one set. All data sets were analyzed using Bartlett's chi-square test for homogeneity to determine whether they met the normality assumptions of the ANOVA. The variances were heteroscedastic ($P < 0.05$) so data were log-transformed before conducting the ANOVA. Analyses were done for both number and weight of captured prawns, but as the results were identical we include only the latter. These ANOVA were: catch by weight of sublegal- or legal-sized prawns in the Pardiac traps and catch by weight of sublegal- or legal-sized prawns in the wire mesh traps.

RESULTS

As a preview of the catch data, retention curves illustrating the sizes of *P. platyceros* captured according to trap

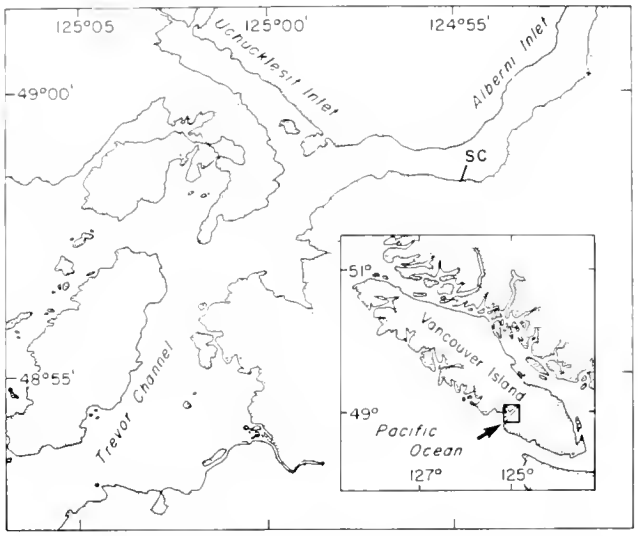

Figure 1. Spencer Creek (SC) experimental prawn fishing site in Alberni Inlet, west coast of Vancouver Island, British Columbia.

type and soak time are provided in Figure 2. Within each of the five trap types the size composition of captured prawns is relatively similar regardless of soak times. Between trap types, however, sizes of retained prawns could vary significantly. The large mesh Pardiac (50-1) and wire mesh (60-1) traps retained fewer sublegal-sized prawns than the small mesh traps (50-0 and 60-0) or the Pardiac trap with the panel of large mesh (50-P). This is also evident in Figure 3 where the mean numbers of sublegal- and legal-sized *P. platyceros* per standardized set are illustrated according to soak time.

The prawn sizes were converted into weights and the resulting ANOVA of catch per standardized set according to trap type are given in Table 2. The only significantly different catches were among sublegal *P. platyceros*. We conducted *a posteriori* Tukey multiple comparison tests (Zar 1984) to identify the variables significantly influencing catches of sublegal prawns. Catches of sublegal prawns in the Pardiac traps were significantly affected by both soak time and trap type. Sublegal catches from 48 h soaks were significantly greater than those for 24 h soaks. There was no significant difference between catches from 72 h and 24 h soaks or from 72 h and 48 h soaks. The 50-1 Pardiac trap type caught significantly fewer sublegal prawns than either the 50-0 or 50-P trap types. There was no difference between the catches of 50-0 and 50-P trap types. Among the two wire mesh trap types, catches of sublegals were significantly affected by both soak time and trap type. A Tukey test of soak time yielded the same results as among the Pardiac traps. The catches of sublegal prawns in 60-1 traps were significantly lower than from 60-0 traps.

DISCUSSION

Minimizing the catch of sublegal-sized crustaceans is desirable because on-board sorting decreases the efficiency of fishing operations and the handling and exposure can cause mortalities (Krouse and Thomas 1975, Crous 1976). Development of "savings gear" in crustacean trap fisheries for escapement of sublegal-sized catch has occurred in crab (*Cancer* spp.) and lobster (*Homarus* spp.) fisheries (Wilder 1945, Krouse and Thomas 1975, Nulk 1978, Brown 1982). We demonstrate here that trap mesh sizes can be effective in savings gear for *P. platyceros* in an industry where there is a legal size limit and as yet no gear restriction (Boutillier 1985b).

Increasing trap mesh size significantly decreased the weight of sublegal prawns caught, but did not decrease the weight of captured legal-sized prawns. Results of varying soak time were inconclusive as to the effects on catches of

TABLE 1.

Characteristics of the five trap types used to capture *Pandalus platyceros* in Alberni Inlet.

	Trap characteristics								
		Dimensions (cm)		Side openings			Mesh characteristics		
Type type*	Shape	Top diameter / Top side × Side height		n	Shape	Internal dimensions (cm)	Type	Diameter (cm)	Size (cm)**
50-0	Round	60 × 24		3	Round	5.5 diameter	Knotted nylon***	0.1	2.4
50-1	Round	60 × 24		3	Round	5.5 diameter	Knotted nylon*	0.1	4.4
50-P	Round	60 × 24		3	Round	5.5 diameter	****	0.1	****
60-0	Square	45 × 24		2	Oval	8.0 × 4.5	Galvanized wire	0.2	2.4 × 1.2
60-1	Square	45 × 24		2	Oval	8.0 × 4.5	Galvanized wire	0.2	2.4 × 2.4

* The 50-series are referred to as "Pardiac" traps and the 60-series as "wire mesh".

** Stretch measure between knots for nylon orside dimensions for rigid galvanized wire mesh.

*** "Herring bunt" mesh.

**** Same mesh as for 50-0 except one side panel (24 × 48 cm) of 50-1 mesh which represented 11.6% of trap surface area.

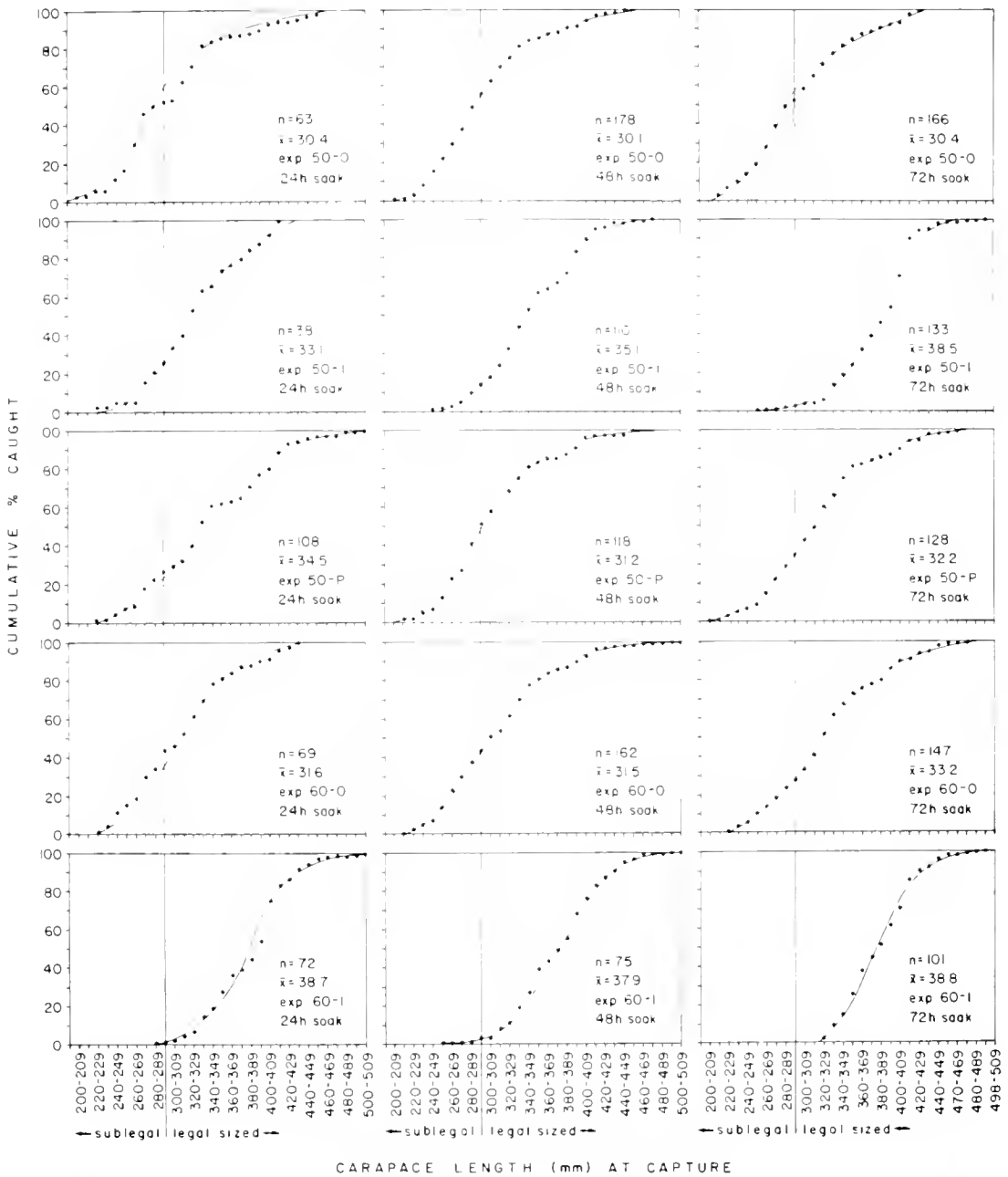

Figure 2. Size composition retention curves for *Pandalus platyceros* catches by trap type and soak time in Alberni Inlet. Numbers of prawns and their mean carapace lengths are provided.

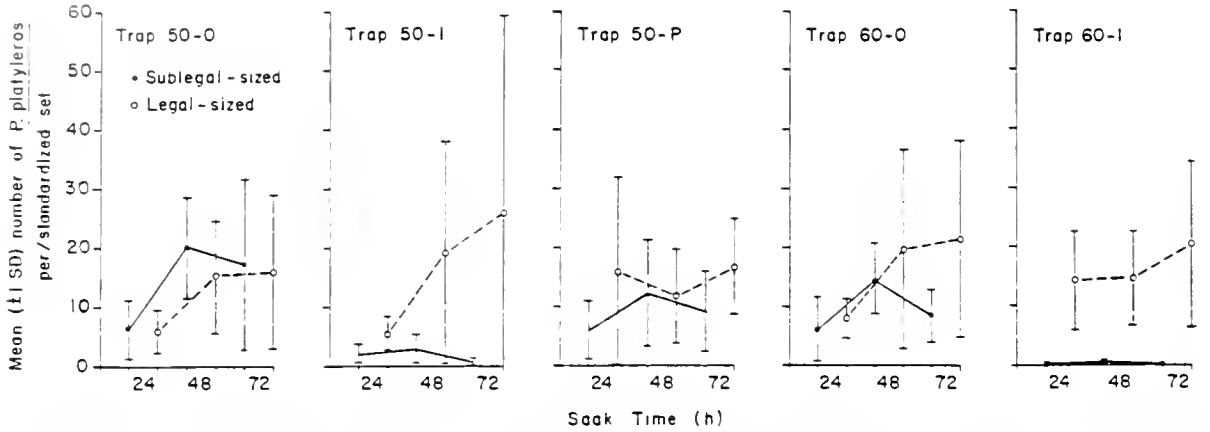

Figure 3. Mean number of legal-sized and sublegal-sized *P. platyceros* caught per standardized set (N = 5 sets) according to trap type at three different soak times.

TABLE 2.

ANOVA results using log of the weight of captured *Pandalus platyceros* as the dependent variable against soak time and trap type.

Trap/Legal size	Source	Degrees of freedom	Mean square	F	P
Pardiac/sublegal	soak time	2	0.3838	4.56	0.0172*
	trap type	2	2.2564	26.80	0.0000*
	soak/trap interaction	4	0.1757	2.09	0.1028
	error	36	0.08422		
Pardiac/legal	soak time	2	0.4011	2.86	0.0704
	trap type	2	0.0980	0.70	0.5037
	soak/trap interaction	4	0.1591	1.13	0.3559
	error	36	0.1403		
Wire mesh/sublegal	soak time	2	0.1791	3.65	0.0414*
	trap type	1	6.9110	140.77	0.0000*
	soak/trap interaction	2	0.0996	2.03	0.1533
	error	24	0.0491		
Wire mesh/legal	soak time	2	0.0814	0.61	0.5510
	trap type	1	0.1825	1.37	0.2533
	soak/trap interaction	2	0.0711	0.53	0.5931
	error	24	0.1332		

* $P < 0.05$

sublegal prawns. Trends are evident in the retention curves where the portion of sublegal catches in saving gear traps 50-1 and 60-1 declines with increasing soak time.

Mesh sizes comparable to the 50-1 and 60-1 traps can be used in *P. platyceros* gear to permit escapement of sublegal-sized prawns, while retaining legal-sized catch. The diagonal measurements of the 50-1 and 60-1 mesh types are 32 and 33 mm respectively; these are similar to the minimum 28.6 mm diagonal measurement used in the Washington State prawn trap fishery (Anonymous 1983).

The industry presently uses more than 13 different general trap types (Boutillier 1985b). The aim will be to implement savings gear regulations within acceptable time-limits. Information on a schedule for implementation may be obtained by gathering annual statistics on the industries' gear loss and replacements.

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FISHERY AND CULTURE OF SELECTED BIVALVES IN MEXICO: PAST, PRESENT AND FUTURE[1]

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ABSTRACT This paper reviews the culture of selected bivalves of Mexico. Most species are utilized locally, but there is potential for some exports. The culture and fisheries of bivalves are often hampered by lack of information and restrictive regulations. *Pinctada mazatlanica* was grown for pearls and pearl shell production in the early 1900s. The methods used for its culture are reviewed. The culture of a few commercial species has shown encouraging results. Over 10,000 kilometers of coastal area with more than 1.5 million hectares of coastal lagoons and bays, plus a subtropical climate, give Mexico a great potential for the development of mariculture.

KEY WORDS: culture, bivalves, Mexico, *Pinctada mazatlanica*

INTRODUCTION

Mollusks are highly valued in Mexico where an abundance and diversity of species can be found all along Mexican coasts.

Most species are exploited locally in artisanal fisheries. There are nine commercial species in the Pacific and California, one in the Caribbean, and one in the Gulf of Mexico (Table 1). Some of these species have been intensively fished for many years with little or no management. Their beds are often overexploited, which together with the degradation of coastal water quality, has made them very scarce.

Though aquaculture in Mexico can be traced back to prehispanic times when the Aztecs reared the "axolotl", a neonatal stage of a salamander, very little has been done in the field of molluscan aquaculture.

THE FISHERIES

History

The use of mollusks for food in coastal communities can be traced back to prehispanic times with the presence of countless shell deposits or middens along both coasts (Schenck and Gifford 1952, Lorenzo 1955, Fieldman 1969, Foster 1975, Reygadas et al. 1984). The diversity of species varies widely and few species can be found throughout Mexico's entire distribution range. These same species are still utilized by coastal people today.

On the Pacific coast of Baja California, the pismo clam, *Tivela stultorum*, predominates in shell deposits. The bay scallop, *Argopecten circularis*, the mother of pearl oyster, *Pinctada mazatlanica*, oyster, *Pteria sterna*, cross-barred chione, *Chione undatella*, and California chione, *C. californiensis*, prevail in the Gulf of California. On the rest of the Pacific coast, the oysters, *Crassostrea palmula* and *C. fisshery*, and the mangrove cockle, *Anadara tuberculosa*, are found. In the Gulf of Mexico only the American oyster, *Crassostrea virginica*, and the mud clam, *Rangia cuneata*, are found in shell middens.

Overview of Techniques

Harvesting methods are primitive. Shellfish are gathered by hand along the shoreline at low tide or subtidally by free diving and by digging with bare hands or forks. On the Gulf of Mexico coast, *Rangia cuneata* is fished with a long pole net from outboard motor boats.

In the Gulf of California, bivalves are gathered by divers, free diving down to 3 m depth and scuba or hooka diving down to 30 m (Figure 1).

Most bivalves are sold fresh in the shell or shipped inland on ice. Scallops and pen shells are shucked in the field (Figure 2) for the adductor muscle which is sold fresh on ice to local markets and frozen for export, primarily to the U.S.A. The Pacific mussel and pismo clam from the Pacific coast of Baja California are the only bivalves canned.

Harvest Statistics

The bulk of the annual harvest of mollusks comes from the Pacific coast (54% in 1977 to 81% in 1981). The Mexican mollusk production is composed of over 50 species, with 9 species exploited intensively (Table 1 and 2). On the Atlantic coast the mud clam, *Rangia cuneata*, has been traditionally intensively exploited along with the more recently exploited reef clam, *Codakia orbicularis*.

Clam production from the different coastal states varies with five states producing over 90% of total landings. Before 1975, production was restricted to five states, but more states have contributed to the harvest in the last decade with both traditional and a few new species.

[1]Contribution number 1444 from the Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062.

Figure 1. Fisherman unloading a bag of scallops into an outboard motor boat equipped with a hooka compressor.

Problems and Potential

The development of a mollusk fishery is hampered by the monoculture approach of fishermen and investors, who are interested only in well commercialized seafood species such as lobsters, shrimp, oysters and fish, ignoring other resources with potential national and international markets. There is a lack of technology for exploiting stocks which are now ignored or not caught by traditional fishing methods.

The lack of information for proper management has led to overexploitation and misuse of stocks.

There are underutilized species that could with proper management be harvested annually, creating employment in new areas.

There is potential for the culture of commercially important species; however, restrictive regulations and difficulty in obtaining necessary water concessions and culture permits have been major constraints for private investors.

CANDIDATE SPECIES FOR CULTURE IN MEXICO

Taxonomy

A candidate species for culture has to satisfy the following requirements:

Figure 2. Shucking camp for scallops.

1. Market acceptability,
2. Competitive price, and
3. Availability of technology for its culture.

There are many species in Mexico that satisfy the first two conditions, along with high price, diminishing stocks and increasing demand. The following species are excellent candidates for culture:

Mangrove cockle *Anadara tuberculosa* (Sowerby 1833)
Pen shell *Pinna rugosa* Sowerby 1835
Atrina maura (Sowerby 1835)
Mother of pearl *Pinctada mazatlanica* (Hanley 1956)
Rock scallop *Spondylus calcifer* Carpenter 1857
Bay scallop *Argopecten circularis* (Sowerby 1835)
Red Clam *Megapitaria aurantiaca* (Sowerby 1831)
Black clam *M. squalida* (Sowerby 1835).

Technology is often the real constraint. Although the general techniques for larval culture developed by Loosanoff and Davis (1963) can be applied to most bivalve species with minor modifications, the specific requirements for every species are different. Culture techniques used for one species in one location are not easily transferred to other species in other places. The general biology and requirements of each species to be cultured should be known to apply the appropriate techniques.

Biology and Ecology

The biology of only a few species has been studied to a limited extent. The growth rates and reproductive cycles of *Megapitaria aurantiaca, M. squalida, Dosinia ponderosa* (Baqueiro and Stuardo 1977), *Argopecten circularis* (Baqueiro et al. 1981), *Anadara tuberculosa* (Baqueiro et al. 1982), *Chione undatella* (Masso and Baqueiro 1984), and *Glycymeris gigantea* (Mucino and Baqueiro 1984) have been determined through studies of natural populations and some studies of marked and caged animals (Table 3). *Pinna rugosa, Argopecten circularis* and *Pinctada mazatlanica* have been studied under culture conditions. Diaz (1972) cultured *P. mazatlanica* in wire cages suspended from rafts, measuring a 9.4% monthly mortality for adults and 6.6% for two to three month old juveniles. Arizpe and Felix (1980) measured growth rate and mortality of spat to two year old *P. rugosa* reared in suspended plastic cages. A 3% mortality occurred in the first year and 1.5% in the second. Growth rate was defined by Von Bertalanffy's equation:

$$L_t = 23.14(1 - e^{0.189\,(t-0.631)})$$

Commercial size of 204 g was attained in two years. Shell length could be converted to weight by the equation:

$$W = 0.0054 \times L^{3.39}$$

Felix et al. (1978) reared spat of *Argopecten circularis* in cages obtaining growth of 3.7 mm per month and 40% mortality in 6 months. A maximum size of 39.5 mm was reached.

TABLE 1.

Bivalves exploited in Mexico and their potential.

Species	Level of Exploitation[a]	Price to Fishermen[b][x]	Aquaculture Potential[c]
California Province (Pacific coast of Baja California)			
Mytilus californianus	C	x 0.30 kg	2
Hinnites multirugosus	C	o 6.00 Kg	1
Tivela stultorum	C	+ 1.60 Kg	3
Panamic Province (Pacific coast and Gulf of California)			
Anadara tuberculosa	C	x 0.07 each	1
A. grandis	L	x 0.15 each	2
A. multicostata	L	x 0.15 each	2
Glycymeris gigantea	P	x	3
Ostrea angelica	P	+	4
Modiolus capax	L	x 0.15 Kg	4
Choromytilus paliopunctatus	P	x 0.15 Kg	4
Mytella strigata	L	x 0.15 Kg	3
Pinna rugosa	C	o 3.00 Kg	1
Atrina maura	C	o 3.00 Kg	2
Pteria sterna	F	o 6.00 Kg	2
Pinctada mazatlanica	F	o 6.00 Kg	2
Pecten vogdesi	C	o 3.00 Kg	2
Argopecten circularis	C	o 2.75 Kg	1
Lyropecten subnudosus	C	o 6.00 Kg	2
Spondylus calcifer	C	o 6.00 Kg	2
S. princeps	C	o 6.00 Kg	2
Laevicardium elatum	L	x 0.15 each	4
Tivela byronensis	L	x 0.15 Kg	4
Trachycardium spp.	L	x 0.15 Kg	4
Megapitaria squalida	C	x 0.15 each	1
M. aurantiaca	C	x 0.15 each	1
Chione spp.	L	x 0.15 Kg	4
Peryglypta multicostata	P	x 0.15 each	4
Ventricolaria isocardia	P	x 0.15 each	4
Caribbean Province (Gulf of Mexico and Caribbean coast)			
Rangia cuneata	C	x 0.08 Kg	1
Asaphis deflorata	L	x 0.25 Kg	4
Chione cancelata	P	+ 1.50 Kg	4

[a] C = commercial exploitation, F = fishing prohibited, L = local use, P = potential; [b]x = whole with shell, + = whole without shell, o = adductor muscle; [c]1 = culture recommended, biology known, 2 = culture recommended, biology unknown; 3 = culture not recommended, biology known; 4 = culture not recommended, biology unknown. [x]dollar exchange rate: 1 U.S. dollar per 200 pesos.

The information so far gathered shows the feasibility of bivalve culture, but many questions on their biology and requirements remain to be answered:

—Optimal densities
—Temperature, salinity, light, pH and oxygen requirements
—Food requirements
—Predators, parasites and diseases.

All these experimental cultures have depended upon natural spawnings of bivalves, but a commercial enterprise could not rely on a source of spat that would be very unpredictable and erratic (Tripp 1978). A commercial endeavor with the bay scallop failed due to unpredictable and erratic setting. Commercial cultures of these species require conditioning, spawning, and larval rearing techniques so that consistent numbers and quality of seed could be produced for culture.

Market

Table 1 shows demand for scallop muscle and similar products and for whole clams in the shell. All of these products are consumer fresh or frozen. The higher priced products have both a national and international market, primarily export to the U.S.A. Scallops are shipped as frozen adductor muscles, and clams are sold as fresh and frozen whole clams. The pismo clam and the Pacific mussel are canned for sale in Mexico or export to the U.S.A. and Japan.

TABLE 2.

Mexican mollusk production by coastal states, 1977–1981 (metric tons).

	1977	1978	1979	1980	1981	%
Baja California	1425	1547	1545	1665	1483	18
Baja California Sur	1053	2028	2742	5875	5117	39
Sonora	89	254	55	118	230	2
Sinaloa	1216	1555	1225	954	1775	15
Nayarit	1	7	58	0	150	1
Jalisco	4	1	0	0	141	1
Colima	0	0	0	62	11	1
Michoacan	0	0	0	0	0	0
Guerrero	22	9	37	0	42	1
Oaxaca	17	0	0	36	20	1
Chiapas	55	60	330	674	80	3
Pacific coast total	3882	5461	5992	9384	9049	78
Tamaulipas	27	0	0	0	0	1
Veracruz	460	614	1023	963	870	9
Tabasco	0	12	0	0	0	1
Campeche	1290	1023	915	1027	1188	12
Yucatan	0	0	0	0	0	0
Quintana Roo	0	0	0	0	0	0
Atlantic coast total	1777	1649	1938	1990	2058	22
National total	5659	7110	9930	11373	11107	

HISTORY OF MOLLUSK CULTURE IN MEXICO

Commercial Endeavors

No commercial culture is being carried out in Mexico at present, but the first record dates back to 1904 in Baja California Sur when a technique was developed to rear the mother of pearl, *Pinctada mazatlanica*, by J. Gaston Vives (Estrada 1916, Townsed 1916, Diguet 1919). Detailed information on this technique was not mentioned by the authors since the whole process was patented. In 1919 the "Compania Criadora de Concha Perla, S.A." obtained a contract from the Federal Government to renew its license with provisions to instruct fisherman in culture, to provide them with up to five million spat of 2 cm length each year, and to manufacture and sell at cost all "protective shields" for oysters. In exchange the company received the right to all waters around Espiritu Santo Island, free import of equipment required for the industry, and the use of private police to guard against poachers.

This contract was expected to renew operations of a firm that had been in operation since 1904, but was destroyed by vandals during the Mexican revolution in 1914. At the time

TABLE 3.

Detected growth of some commercial species.

Species	Growth (mm/month)	Source
Megapitaria squalida	5.5 (+) 3 (−)	Baqueiro and Stuardo, 1977
M. aurantiaca	4.5 to 6 (+) 3 (−)	Baqueiro and Stuardo, 1977
Dosinia ponderosa	2.3 (+) 2 (−)	Baqueiro and Stuardo, 1977
Anadara tuberculosa	4 to 6 (+)	Baqueiro et al., 1982
Chione undatella	2 (+)	Masso and Baqueiro (in press)
Argopecten circularis	2 to 4 (+)	Baqueiro et al., 1981
	3.7 (−)	Felix, 1978
Pinna rugosa	10 (−)	Arizpe and Felix, 1984
Glycymeris gigantea	5 (+)	Musino and Baqueiro (in press)

(+) from natural populations, (−) from experimental cultures.

Figure 3. Aerial view of artificial lagoon and nursery canals with palm roofs to prevent over heating of juvenile pearl oyster, *Pinctada mazatlanica*.

Figure 4. Nursery canals for the culture of juvenile pearl oysters, *Pinctada mazatlanica*. Note sluice gate to control tide flow and the passage of predators.

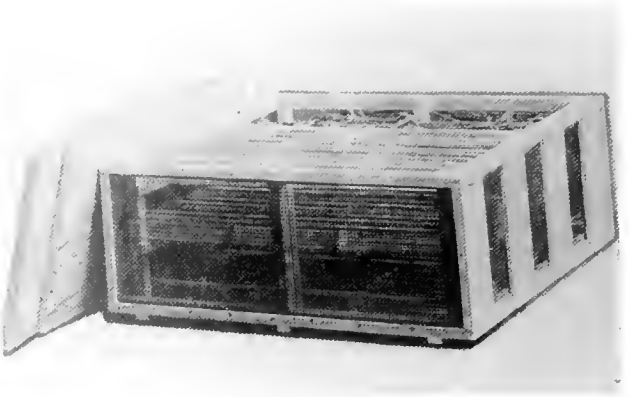

Figure 6. Collectors of hatchers showing wire mesh sides, inner compartments and solid board top that aided flotation.

of its destruction, the firm produced five million pearl oysters of one to three years of age, utilizing over 500 spat collectors and employing 400 workers.

The technique is described in detail in the contract and patents but was never made public. Mr. J. Gaston Vives Jr., surviving son of Mr. J. Gaston Vives Sr., furnished all available information on the Company and allowed us to describe the technique used by a once flourishing mother of pearl culture industry.

Spat were collected by means of "hatchers" which were wooden frames covered with galvanized wire mesh, the top of the hatcher being a solid board to provide shade and flotation (Figures 5 and 6). These cages or boxes were 3 m long, 2 m wide and 1 m high. Inside these hatchers were wooden trays (nests) where shells, branches and other objects were placed as cultch for the spat. The hatchers were floated just below the water surface from March to June. In each hatcher approximately 50 adult mother of pearl oysters were placed. Ten to twenty thousand spat one to two cm long were collected from each hatcher.

Spat were picked by hand from the hatcher nests and laid on the bottom of "nursery canals" (Figures 7 and 8). These consisted of 36 masonry canals, 25 m long, 5 m wide and 3 m deep, connected at opposite ends to form a zigzag pattern with one end opening to the sea and the other to an artificial lagoon made by a dyke 500 m long, 11 m wide and 10 m high (Figures 3 and 4). Both ends opened through a sluice containing wire mesh screens to control the water level and exclude predators. The canals were shaded by palm roofs to prevent overheating at low tide.

When the pearl oysters reached 3 to 4 cm in length, they were scattered on the bottom of the canals and provided with stones and shells for byssal attachment and protection.

After 6 to 8 months when the oysters reached about 5 cm in length, they were transplanted to prepared bottoms on the open sea. Live oysters were transported from the nursery to the growing grounds in specially designed cages (Figure 9) that were towed by sailboats. One hundred twenty hectares of sandy sea bottom around Espiritu Santo Island were covered with stones and shells to provide firm substrate by byssal attachment by the pearl oysters. This was done by hard-hat divers (Figure 12).

To protect the mother of pearl oysters from predators, a tin shield ("protective shield") (Figure 10) was cemented to the upper shell by a glue made from the sap of two local

Figure 5. Hatchers, collecting boxes for spat of pearl oysters, stowed between seasons.

Figure 7. Workers picking pearl oyster spat from inner compartments of hatchers.

Figure 8. Nursery canal with wire mesh trays on the bottom, holding pearl oyster spat.

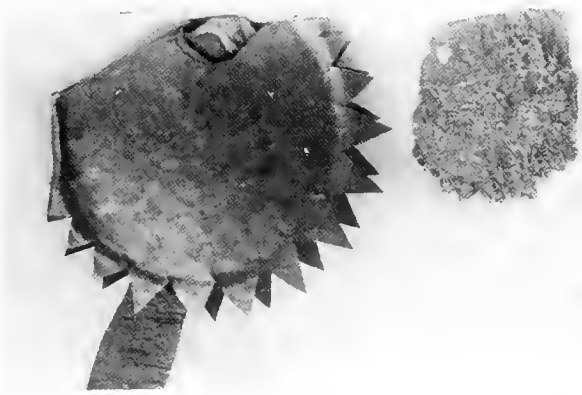

Figure 10. Juvenile pearl oyster with protective tin shell to prevent predation. Note wooden slab that acted as rudder on its fall from the boat and opening for attachment of the byssus.

species of trees. On top of the shield was a cork or small wooden slab which held the oyster in a straight up position during its descent to the bottom and until it had attached by its byssus.

A "protective pavilion" (Figure 11) was also developed to use soft sands and muddy bottoms. It was constructed of a concrete slab 60 cm long, 30 cm wide, 15 cm high, covered by a galvanized wire-mesh cage. Fifty to 60 oysters were placed in each cage where they grew for two years with only a 30% mortality. The cages and nursery boxes were reconditioned with a galvanic bath every season for reuse.

The oysters were grown for two to three years for the nacre or mother of pearl shell and the pearls. Oysters were harvested by divers. At the time of the company's demise, 1.5 million shells were produced annually.

A repletion program was initiated with the mud clam, *Rangia cuneata*, that had been heavily exploited in the Gulf of Mexico. The discovery in 1970 of abundant stocks of juveniles led to the practice of bed management. Overcrowded beds of small clams were thinned by transplanting clams to overexploited or depleted commercial beds. This has sustained a stable fishery at Pom and Atasta lagoons, Campeche (Figure 13).

Based on two years of government-sponsored experi-

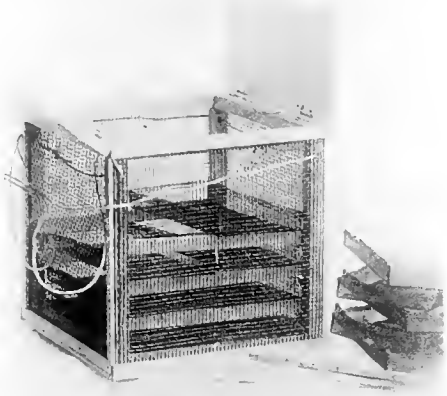

Figure 9. Transportation cage. Pearl oysters on wire mesh trays were placed in transportation cages and towed by sailboats to the rearing grounds.

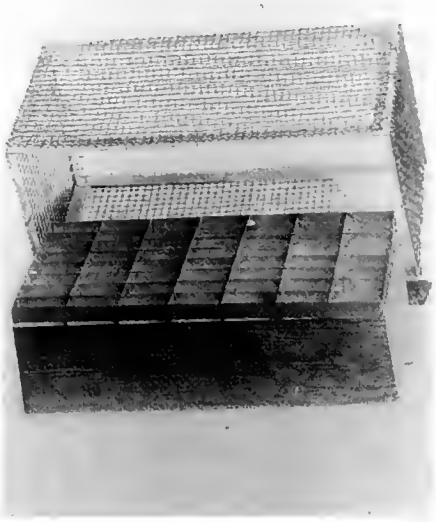

Figure 11. Concrete block with compartments for individual pearl oysters and protective wire-mesh cage. Used on sandy and muddy bottoms.

Figure 12. Hard hat divers were used to prepare bottoms with stones and lay culture devices.

mental culture of the bay scallop, *Argopecten circularis*, a commercial farm was started in La Paz, Baja California Sur (Figure 13). This scallop venture relied on collection of spat from natural sets. Poor settlement during the second year of operation forced this enterprise to close.

Culture Research

Research on the culture and biology of mollusks has been sparse and erratic (Baqueiro 1984). Diaz (1972) reared *Pinctada mazatlanica* in suspended wire cages and baskets. In the same locality, Martinez (unpublished) planted *Pinna rugosa* juveniles to study growth and survival. Results were inconclusive due to lack of continuity.

In 1977 the Fisheries Department, through its aquaculture office in La Paz, Baja California Sur, began research on larval abundance, collecting devices, and on growth and survival of several species under different culture conditions (Tripp, 1978).

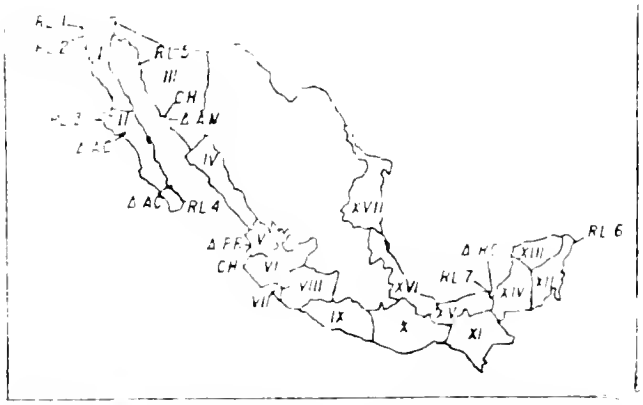

Figure 13. Map of Mexican coastal states: I–Baja California, II–Baja California Sur, III–Sonora, IV–Sinaloa, V–Nayarit, VI–Jalisco, VII–Colima, VIII–Michoacan, IX–Guerrero, X–Oaxaca, XI–Chiapas, XII–Quintana Roo, XIII–Yucatan, XIV–Campeche, XV–Tabasco, XVI–Veracruz, XVII–Tamaulipas. △ Localities where clams are or have been cultured: AC–*Argopecten circularis*, AM–*Atrina maura*, PR–*Pinna rugasa*, RC–*Rangia cuneata*. CH–commercial hatcheries: 1–Kino Bay, 2–San Blas. RL–research laboratories: 1–Ensenada, 2–Erendira, 3–Tortugas Bay, 4–La Paz, 5–Puerto Penasco, 6–Puerto Morelos, 7–Del Carmen Island.

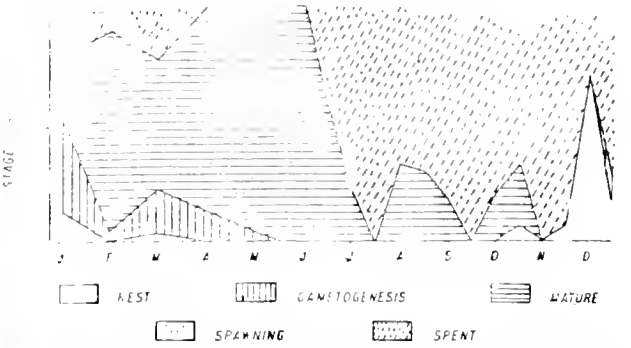

Figure 14. Reproductive cycle of *Rangia cuneata* from Pom lagoon, Campeche, during 1974. Adapted from Rogers and Garcia-Cubas (1981).

Felix et al. (1978) studied growth and survival of bay scallops, *Argopecten circularis*, in suspended plastic cages. Arizpe and Felix (1984) determined growth and survival of pen shells, *Pinna rugosa*, in suspended cages and fenced bottom cultures.

There are two commercial hatcheries on the Pacific coast (Figure 13) where pen shells, *Pinna rugosa* and *Atrina maura*, have been reared experimentally from egg to commercial size. They are reared to 10 mm after settlement and then transferred to either open tanks or to suspended cultures, using in both cases Nestier® plastic trays to hold them for three to four months before being planted on the bottom (Flores, per. comm.).

GAMETOGENESIS AND SPAWNING IN MEXICAN CLAM POPULATIONS

A three-year gametogenic study of *Rangia cuneata* has been reported for a single locality in the Gulf of Mexico (Rogers and Garcia-Cubas 1981) (Figure 14). More species have been studied on the Pacific coast. *Anadara tuberculosa* (Flores 1971, Baqueiro et al. 1982) (Figure 15) and *Pinna rugosa* (Noguera and Gomez 1972, Coronel 1981) (Figure 21A, B) were studied in different localities at different times; *Mitella strigata* (Estevez 1975) (Figure 17A, B) presented different reproductive trends in response to different climatic conditions between localities.

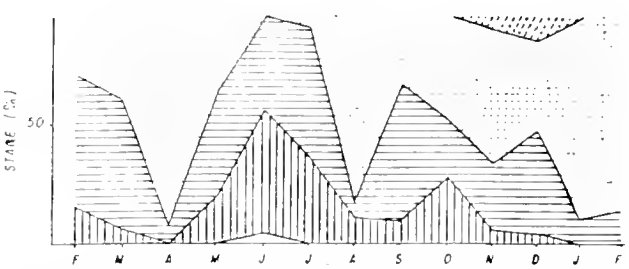

Figure 15. Reproductive cycle of *Anadara tuberculosa* from La Paz, Baja California Sur, during 1978–1979 (Baqueiro et al. 1984).

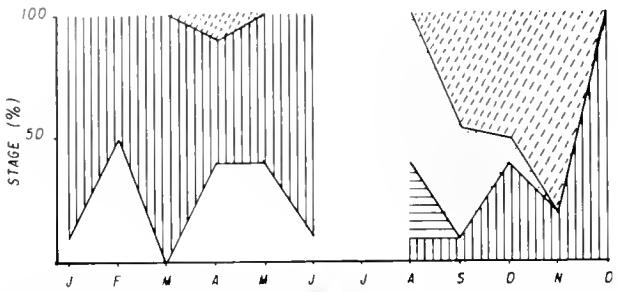

Figure 16. Reproductive cycle of *Mytella strigata*. a) Nuxco, b) Chautengo, Gro. during 1974 (Estevez 1975).

Populations in open tropical waters or in coastal lagoons from the desert area of Baja California Gulf Coast are exposed to a very stable environment without strong seasonal fluctuations. Gametogenesis continues throughout the year, which is reflected in constant spawning with two or three peaks a year (Figures 14, 17A, B, 18B, 19, 21B). Populations that inhabit coastal lagoons or shallow bays on the Pacific coast of Baja California, where the seasonal effect of climate can be felt, have a well defined reproductive period with gametogenesis either throughout most or all year (Figures 15, 16a,b, 17a,b, 18b,c, 19).

Both groups can present either a clear post-spawning and rest period after a spawning peak or have a very quick gonad recovery with no clear post spawning or rest period.

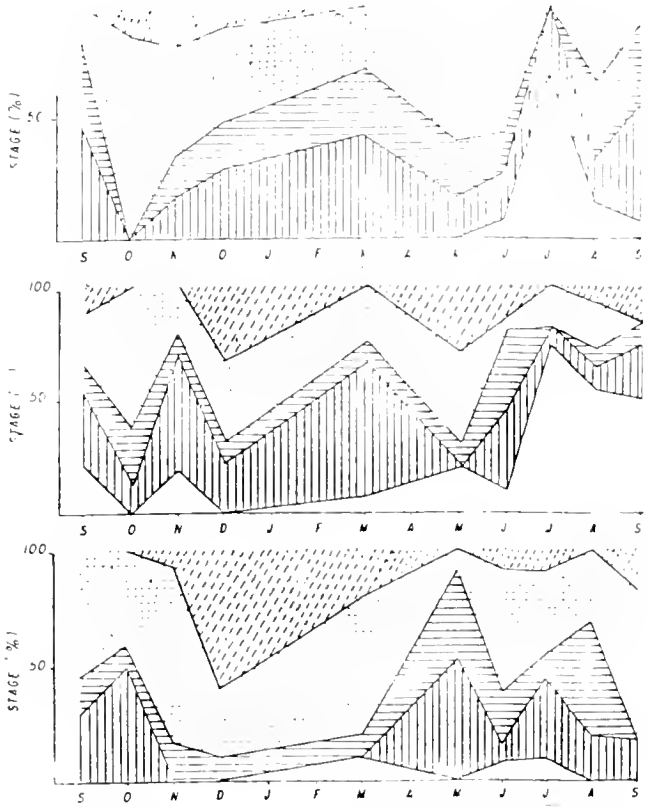

Figure 17. Reproductive cycle of *Megapitaria squalida* (a), *M. aurantiaca* (b) and *Dosinia ponderosa* (c) from Zihuatanejo, Gro. during 1974–1975 (Baqueiro and Stuardo 1971).

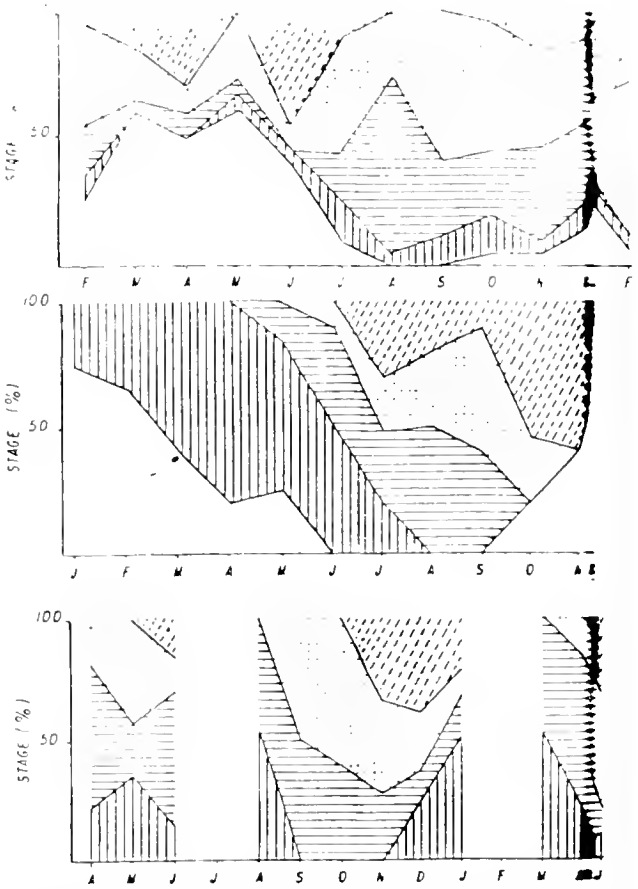

Figure 18. Reproductive cycle of (a) *Chione undatella* from La Paz Bay, Baja California Sur during 1978–1979 (Masso and Baqueiro 1984); (b) *Pinctada mazatlanica* from Mazatlan, Sinaloa during 1967 (Sevilla 1969); (c) *Glycymeris gigantea* from Concepcion Bay, Baja California Sur during 1979–1980 (Mucino and Baqueiro 1984).

BIOLOGY AND CULTURE OF *ARGOPECTEN CIRCULARIS* AND *PINNA RUGOSA*

The bay scallop, *Argopecten circularis*, and pen shell, *Pinna rugosa*, are two species whose biology and culture have been most studied. A pilot scale culture and at least one commercial culture of *A. circularis* has been carried out (Ortiz 1979).

Both species are found in the Panamic province. *Argo-*

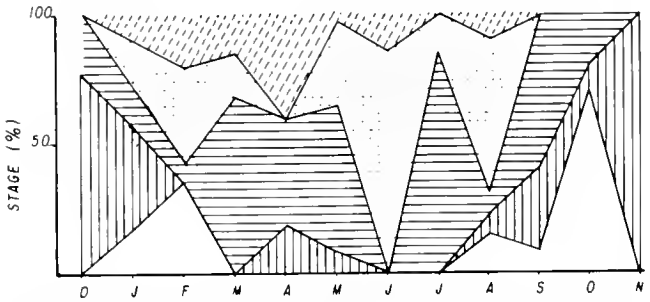

Figure 19. Reproductive cycle of *Argopecten circularis* from La Paz Bay, Baja California Sur during 1978–1979 (Baqueiro et al. 1981).

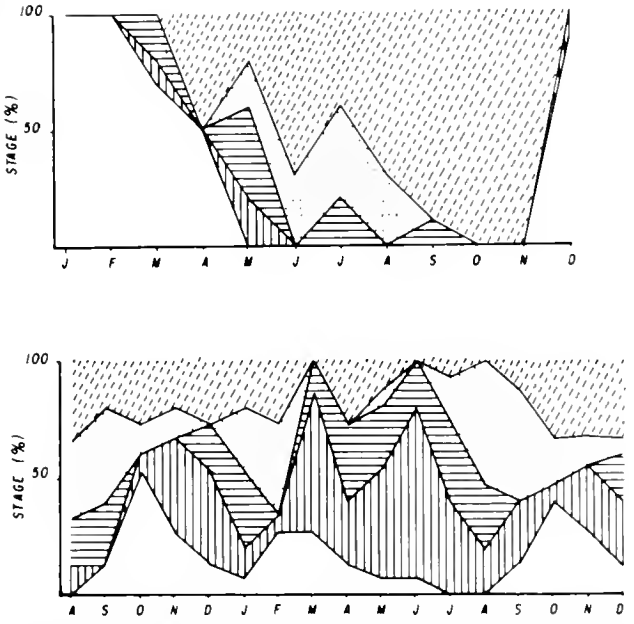

Figure 20. Reproductive cycle of *Pinna rugosa* from La Paz Bay (a) during 1969 (Noguera and Gomez 1972), (b) during 1980 (Coronel 1981).

pecten circularis has a range from Cedres Island, Baja California throughout the Gulf of California to Paita, Peru (Keen 1971). It is found on sea grass or intertidal algal beds to depths of 135 m, but is more abundant between 1 and 6 m depth in coastal lagoons and well protected bays. *Pinna rugosa* ranges from southern Baja California, Gulf of California to Panama on a wide variety of bottom types from sandy-mud to boulders in both open sea and coastal lagoons in depths of 2 to 45 m, but is more abundant in protected bays with good oceanic water circulation on muddy-sand bottoms.

The growth, reproduction and reproductive cycles of natural populations of *A. circularis* were studied by Baqueiro et al. (1981) and Yoshida and de Alva (1977). Larval abundance in plankton and settlement in different types of collectors were determined by Tripp (1978). Growth and survival in plastic cages were studied by Felix et al. (1978).

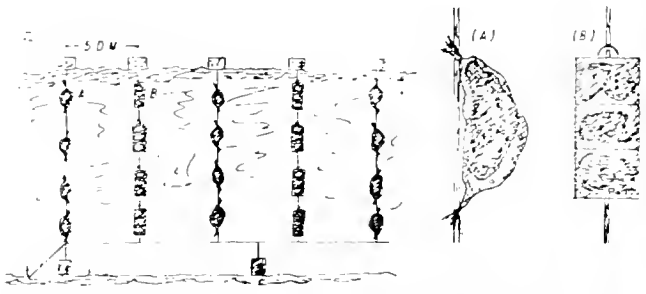

Figure 21. Collectors used to catch spat of *Argopecten circularis* and *Pinna rugosa*. a) Plastic net bag with brush branches, b) Plastic mesh basket with shells, c) Long line of collectors (Felix et al. 1978).

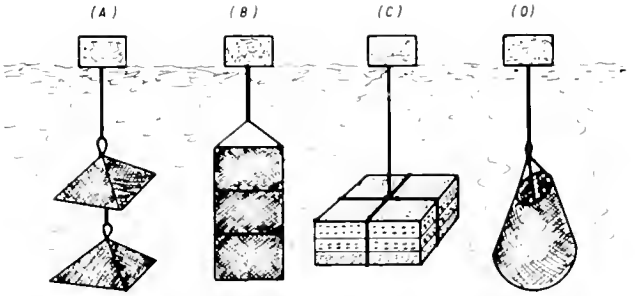

Figure 22. Different structures for rearing *Argopecten circularis* and *Pinna rugosa* juveniles. a) Modified lantern, b) Three layer basket, c) Nestier® trays, d) Net bag (Felix et al. 1978).

This species has a very active gametogenic cycle (Figure 19) which shows a fast recovery from spawning. The availability of ripe gonads during most of the year allows a long reproductive season with three peaks a year. This permits an almost constant recruitment, and natural sets of spat can be collected at three peak times a year.

Growth rate of natural populations varied from 2 to 4 mm a month. In cage culture the growth rate was 3.7 mm a month in the first eight months after which growth ceased, perhaps due to overcrowding in the cages.

Survival in cages was 40% in 8 months. In natural populations the production rate of biomass was estimated over a year to average 55.4 g/m^2/month, with a maximum of 119 g/m^2. Scallops in suspended cage culture obtained a maximum of 37.5 g/m^2/month.

Pinna rugosa has not been studied in its natural populations except for its reproductive cycle (Noguera and Gomez 1972, Coronel 1981). The growth rate for the first two years of *P. rugosa* kept in pens or suspended in Nestier® trays was determined by Arizpe and Felix (1984).

The reproductive cycle determined by Coronel (1981) (Figure 20b) shows an active gametogenesis throughout the year with ripe gonads from March to September and two reproductive periods, one from June to November-December and a secondary period from January to March. This differs from the findings of Noguera and Gomez

Figure 23. Multilayer rearing basket for suspension culture of *Pinna rugosa* (Arizpe and Felix 1984).

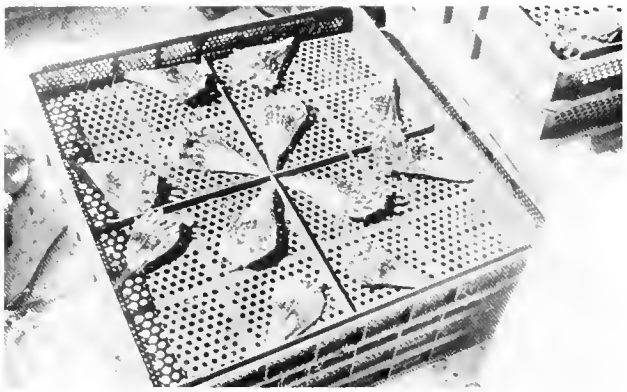

Figure 24. Two-year-old pen shell, *Pinna rugosa*, reared in Nestier® trays (Arizpe and Felix 1984).

(1972) (Figure 20a) where gametogenesis was restricted from March to June and setting from May to September. Both studies suggest a rapid conditioning period. Noguera and Gomez's data suggested a rest period which was not evident in Coronel's work.

Growth rate under culture conditions was 1 cm a month for the first two years. Arizpe suggested an optimum harvest age of 12 to 14 months.

Culture Techniques

Conditioning of *A. circularis* was attained in a laboratory in four weeks at 22°C, using running seawater and one daily supplementary feeding of 1.25×10^6 cells/ml of *Isochrysis* sp. Spawning was induced by thermal shock, raising the water temperature from 20° to 28°C in two hours. Metamorphosis of larvae started on the 20th day at 22°C.

For the pilot culture of *A. circularis*, spat are collected from the field with collectors made of plastic net bags filled with shells or branches (Figure 21). Larval abundance was determined by plankton tows, and collectors were dispensed when a high abundance was observed. When the spat reached 5 to 8 mm in size, they were scraped off the collectors and placed in Nestier® trays with mosquito net liners at 2000 spat per tray, occupying about 50% of the tray surface.

Trays were stacked in groups of five and hung from rafts or long lines at 1 m depth. Fouling was a major problem, requiring cleaning about every two weeks. Trays were scrubbed with a brush or sprayed with a water jet from a motor-driven pump. Mortality kept spat density equal or under 50% of total tray area. When the scallops reached 30 to 35 mm, their growth stopped and their shells thickened, increasing to width but not in length, and their meat condition was very poor.

Pinna rugosa spat are collected and handled like the bay scallop. Confinement in trays did not seem to have any adverse effects on them in the two years it took to reach commercial size (Figures 23, 24).

Pinna rugosa and *Atrina maura* from San Blas, Nayarit and Kino Bay, Sonora were collected ripe from the field and induced to spawn with thermal shock. Their larvae were reared in metamorphosis in 18 to 20 days. After metamorphosis they were kept in Nestier® trays in open tanks with running seawater or suspended from rafts and long lines until they reached 6 to 7 cm, after which they were transplanted to the bottom in protected ponds. Commercial size was reached in two years (Flores, per. comm.).

SUMMARY

Culture techniques have copied oyster culture in other countries. The slow growth and stunting of *A. circularis* show the need for research on culture methods. The lack of technical information has hindered the development of mariculture. Previous failures discourage others until a well proven technique can be demonstrated.

Legislation to protect water parcels or leases and culture stock is needed to enhance aquaculture in Mexico. A simplification of licensing and leasing regulations by assigning them to a single agency would be useful. At present it involves no less than four ministries to get an aquaculture permit and permits to use a body of water.

The present fisheries law states those given a permit to exploit a resource should improve it by aquaculture. The Fisheries ministry tries to accomplish this by providing training and counseling to fishermen. With an education program in aquaculture sponsored by the Education ministry from secondary school through college, aquaculture is expected to boom in the coming years.

The culture of a few commercial species has shown encouraging results. As techniques are developed, the advantage of a year-round growing season and available labor will certainly aid in the development of an industry which will provide jobs, income and food for both local use and export.

Many large species like the pen shell, rock scallop and red clam do not have to be grown to full size since they can be sold to foreign markets that demand small and medium size scallops and clams, taking advantage of the faster growth in their first years of life.

Over ten thousand kilometers of coastal area, with more than a million and a half hectares of coastal lagoons and protected bays, give Mexico a great potential for the development of mariculture. Since clams and scallops are among the easiest and the highest priced species to culture, their culture should be encouraged.

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ALTERNATIVE TREATMENTS TO PREVENT THE BIODETERIORATION OF OFFSHORE WOOD LOBSTER TRAPS BY THE WOOD-BORING BIVALVE, *XYLOPHAGA ATLANTICA*

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ABSTRACT Wood traps utilized by lobstermen on the outer continental shelf of the northwest Atlantic Ocean are susceptible to destruction by the wood-boring bivalve *Xylophaga atlantica*. Preservatives have traditionally been used to protect wood from biofouling organisms. The effectiveness of three alternative treatments that would kill recently settled juvenile *Xylophaga* prior to the destruction of the wood was examined. The treatments included heated sea water, a chlorine bleach solution and a sodium chloride brine solution. While most treatments caused significant mortality, a saturated brine solution (265‰) proved to be the most effective and practical treatment. A 30-sec treatment affected a 99% mortality of *Xylophaga* on panels exposed at sea for 30–45 days. A 60-sec treatment affected a 100% mortality of *Xylophaga* on panels exposed at sea for 60–75 days.

KEY WORDS: wood lobster traps, *Xylophaga atlantica*, biodeterioration

INTRODUCTION

The offshore lobster fishery in the northwest Atlantic Ocean has been plagued by *Xylophaga atlantica* Richards, a deep-sea, wood-boring bivalve which readily destroys untreated wood lobster traps (Dow 1950, Dow and Baird 1953, Culliney and Turner 1976). Traps are usually constructed of wood, specifically red oak, although vinyl-covered wire mesh traps have recently been introduced into the fishery. Wood traps remain the preferred method of most offshore lobstermen because of their low initial cost, repairability, perceived higher catch rates, and potentially longer length of service.

Wood, however, is subject to attack by wood-boring bivalves and untreated or non-preserved traps are often totally destroyed in less than one year (Dow 1950, Prudden 1962). Lobstermen have treated their traps with various preservatives including tar, copper paint, chromated zinc chloride, creosote, and other substances in order to prevent the infestation by wood-boring bivalves (Prudden 1962). Fisherman in recent years, have been using a solution based on Bis-Tri-N-Butyltin Oxide (Wilder and Walsh 1968). This pesticide solution, although reasonably effective in preventing the infestation of borers and in controlling biofouling of the traps, has some potential human health hazards associated with its use (Schweinfurth and Gunzel 1987). The EPA is presently reviewing the use of tributyltins (TBT's) in antifouling paints, and plans to expand this investigation to all applications of TBT's in the marine environment (Lydecker 1986, Simpson 1986). Recent studies document that TBT's in the marine environment constitute a hazard to various organisms. TBT's accumulate in tissues of fish and shellfish (Laughlin 1986), and they often result in poor growth rates, reduced reproductive success, and death (Thain 1986). The long-term effects of TBT-treated traps on lobsters that are captured and released have not been investigated.

Traps annually treated with wood preservatives last three to four years. However, transporting traps to shore, drying them, and retreating with a wood preservative is costly. Additionally, because the preservatives leach out of the wood, infestation by *Xylophaga* inevitably occurs and results in trap deterioration. Offshore lobstermen speculate that a wood trap would last six to eight years if a 100% effective method could be developed to prevent damage due to wood-boring bivalves.

Because of the deleterious effects on the marine environment of the various wood preservatives available to lobster trap fishermen, an alternative strategy was investigated to prevent the development of *Xylophaga* in wood traps using periodic at sea treatments that would affect at least a 98% mortality on recently settled juveniles. The purpose of the experiments was to identify alternative treatments that would accomplish this objective. The selected treatment would have to be both effective and safe, simple and rapid; the treatment would have to be administered sufficiently often so as to minimize destruction of the wood by the recently settled juvenile boring bivalves.

PREVIOUS WORK

The problem of the infestation of wood lobster traps by the marine borer, *X. atlantica*, must be solved by biofouling prevention or periodic control. Wood products used in coastal marine applications are usually treated with a preservative to prevent biofouling and general deterioration

caused by bacteria, fungi, *Limnoria* (a crustacean), and bivalve borers (shipworms). The preservatives are long-term, and are applied under pressure to ensure the penetration of the chemical into the wood. The most universal of these treatments is creosote, however other chemicals are also used, including copper sulfate, pentachlorophenol, and others [for a list of previously used substances, see references in Clapp and Kenk (1963)]. Wood preservatives in general act either to prevent the settlement of fouling organisms on the treated substrate or to kill the recently settled animals through an accumulation of the toxic chemical. Anti-fouling bottom paints or coatings act in a similar manner, although these are superficial treatments, rather than impregnated into the wood.

In contrast to these long-term prevention methods biofouling can also be controlled by periodically applying a short-term lethal dose of biocide. These treatments may be used to kill plants and animals that have recently fouled surfaces. Biocides have been especially useful in the control of fouling organisms that clog the intake and condenser systems of thermal-electric power plants (Morgan and Carpenter 1978, Hillman 1980). In plants which use once-through cooling, chlorine gas or sodium hypochlorite is one of the safer and more economical biocides.

Heated water can also be used periodically to treat surfaces to control biofouling, and some power plants recirculate on a weekly basis heated water to increase the system temperature to 51° C (Stock and Strachan 1977). This heat effectively kills biofouling organisms. Some Maine lobstermen use engine-heated water in a dip tank to control biofouling on lobster trap warp and buoys.

A hypersaline solution is also an effective biocide that has been considered for control of marine biofouling invertebrates (Kinne 1971). A Massachusetts lobsterman reported that a brine solution successfully controls biofouling on lobster trap warps and buoys.

MATERIALS AND METHODS

Recently settled juvenile *Xylophaga* were collected from the southern New England outer continental shelf using wood test panels. Half of the 12 × 20 × 2.5 cm panels employed were softwood, clear white pine, and half were hardwood, clear red oak. Two racks of 24 wood test panels each were placed in eight vinyl-coated wire mesh traps. Four traps were deployed at a relatively shallow (73 m) offshore location, while the other four traps were deployed at a relatively deep (165 m) offshore site. At each location a cluster of two experimental traps were included on each of two trawls of traps, allowing each trawl to be considered a replicate and providing insurance that data collection would continue in the event of trap loss.

The wood panels remained submerged for periods of one, two, three, and five months. On removal from the water the racks were transported to shore in the circulating sea water tanks of the lobster boat, and then placed in circulating chilled seawater (10°C) in the laboratory. The panels were acclimatized for a period of five to seven days and then divided into experimental and control groups.

All panels were examined using a dissecting microscope, and live juvenile *X. atlantica* were individually identified. The experimental panels were exposed to treatments of varying composition, concentration, temperature, and duration. The control panels were treated in chilled sea water (10°C) for 90 sec. After a second period of five to seven days of acclimatization the panels were examined and the percent *Xylophaga* mortality determined. The presence of siphon activity was used to determine the animal condition.

A variety of treatments were initially considered including heated water, chlorine bleach solution, brine solution, microwave radiation, ultrasonic vibrations and others. However, only three treatments methods were exhaustively tested because of the at-sea practicality criteria. Panels exposed at sea for 30–45 and 60–75 days were treated with heated sea water at 100, 82, 65, 49 and 32°C for durations of 30, 60 and 90 seconds. Panels exposed at sea for 30–45 and 60–75 days were treated with 100, 50 and 25 percent chlorine bleach solutions for durations of 30, 60 and 90 seconds. The 100% chlorine bleach solution is 5.25% sodium hypochlorite. The dilutions were made with seawater. Panels exposed for 30–45 and 60–75 days were treated with sodium chloride brine solutions that were concentrated at 100, 75 and 50% of saturation at 5 and 20°C. The treatment durations were 30, 60 and 90 seconds. The 265‰ sodium chloride solution is saturated at 16°C. The dilutions were made volumetrically with seawater, and verified with a hydrometer reading % saturation.

Increased panel exposure time resulted in infestations of more developed animals, and therefore would presumably require a treatment of longer duration or greater intensity.

The data were grouped according to treatment method and wood type. A t-test for paired comparisons (Sokal and Rohlf 1981) was used to investigate differences in the effectiveness of treatments on wood type. Similarily, a t-test for paired comparisons was used to detect differences in the effectiveness of the brine solution treatments at different temperatures. In both comparisons, the null hypothesis, that there was no difference in either wood type or brine solution treatment temperature, was rejected at an $\alpha = 0.01$. The effectiveness of the pooled treatment data was compared to the control treatment data using a chi-square test for goodness of fit at an $\alpha = 0.01$ (Sokal and Rohlf 1981).

RESULTS

The results of the t-test for paired comparisons indicated no significant difference in treatment effectiveness due to wood type or brine solution temperature (Table 1). All data for the pine and oak were pooled using weighted averages. In addition, the data for the brine solution treatments at 20

TABLE 1.

Results of t-test for paired comparisons.

Treatment	Panel Exposure	Comparison	Number of Panels	T-Stat
Brine 20°C	30–45	Pine/Oak	10	1.25
Brine 5°C	30–45	Pine/Oak	10	1.84
Brine	30–45	20° 5°C	10	1.76
Brine 20°C	60–75	Pine/Oak	10	2.40
Brine 5°C	60–75	Pine/Oak	10	1.87
Brine	60–75	20°/5°C	10	0.67
Chlorine Bleach	30–35	Pine/Oak	10	2.27
Chlorine Bleach	60–75	Pine/Oak	10	1.23
Heated Water	30–45	Pine/Oak	10	1.44
Heated Water	60–75	Pine/Oak	10	1.14

For N = 10 and α = 0.01, the t-stat is 3.25.

and 5°C were pooled using weighted averages. The pooled treatment data were compared to the control treatment for each group of experiments and the statistically significant treatments identified (Tables 2, 3 and 4). For each of the treatment methods, a 98% mortality isopleth was determined for the significant data points (Figures 1, 2 and 3). Treatments on or above that curve meet the minimum effectiveness requirement. The heated water treatments

TABLE 2.

Results of the heated water treatments on panels exposed for 30–45 and 60–75 days.

Treatment (°C)	Duration (sec)	Panel Exposure (days)	Number of Juveniles	Mortality (%)
100	30	30–45	36	100**
100	60	30–45	23	100**
100	90	30–45	32	100**
82	30	30–45	29	100**
82	60	30–45	28	100**
82	90	30–45	25	100**
65	30	30–45	41	100**
65	60	30–45	30	100**
65	90	30–45	40	100**
49	30	30–45	30	0
49	60	30–45	22	35**
49	90	30–45	17	50**
32	30	30–45	30	3
32	60	30–45	37	11
32	90	30–45	24	0
control	90	30–45	32	3
100	30	60–75	46	100**
100	60	60–75	41	100**
100	90	60–75	41	100**
82	30	60–75	51	100**
82	60	60–75	43	100**
82	90	60–75	43	100**
65	30	60–75	101	94**
65	60	60–75	99	100**
65	90	60–75	93	100**
49	30	60–75	54	4
49	60	60–75	48	20**
49	90	60–75	48	87**
32	30	60–75	45	0
32	60	60–75	56	2
32	90	60–75	77	1
control	90	60–75	95	6

** Indicates a treatment effect significantly different from the control group, α = 0.01.

TABLE 3.

Results of the chlorine bleach treatments on panels exposed for 30–45 and 60–75 days.

Treatment (% solution)	Duration (sec)	Panel Exposure (days)	Number of Juveniles	Mortality (%)
100	30	30–45	27	100**
100	60	30–45	29	100**
100	90	30–45	31	100**
50	30	30–45	30	87**
50	60	30–45	25	100**
50	90	30–45	33	100**
25	30	30–45	26	38**
25	60	30–45	27	67**
25	90	30–45	24	83**
control	90	30–45	27	15
100	30	60–75	67	94**
100	60	60–75	72	100**
100	90	60–75	64	100**
50	30	60–75	71	78**
50	60	60–75	60	88**
50	90	60–75	60	90**
25	30	60–75	70	60**
25	60	60–75	50	61**
25	90	60–75	65	66**
control	90	60–75	75	8

** Indicates a treatment effect significantly different from the control group, $\alpha = 0.01$.

proved extremely effective from 100 to 65°C, providing a greater than 98% mortality on *Xylophaga* infested panels exposed for both 30–45 and 60–75 days (Figure 1). The chlorine bleach solutions were also effective biocides on the juvenile *Xylophaga* infested on panels exposed for 30–45 and 60–75 days. Full strength chlorine bleach affected a 100% mortality with a 30-sec treatment on panels exposed for 30–45 days and with a 60-sec treatment on panels exposed for 60–75 days. The brine solution treatments were also effective at killing the juvenile *Xylophaga*.

TABLE 4.

Results of the brine solution treatments on panels exposed for 30–45 and 60–75 days.

Treatment (% saturation)	Duration (sec)	Panel Exposure (days)	Number of Juveniles	Mortality (%)
100	30	30–45	123	99**
100	60	30–45	145	99**
100	90	30–45	136	100**
75	30	30–45	131	88**
75	60	30–45	132	97**
75	90	30–45	131	99**
50	30	30–45	108	53**
50	60	30–45	146	80**
50	90	30–45	142	88**
control	90	30–45	136	6
100	30	60–75	71	76**
100	60	60–75	61	100**
100	90	60–75	64	100**
75	30	60–75	73	67**
75	60	60–75	71	76**
75	90	60–75	75	89**
50	30	60–75	70	11**
50	60	60–75	64	16**
50	90	60–75	53	37**
control	90	60–75	66	0

** Indicates a treatment effect significantly different from the control group, $\alpha = 0.01$.

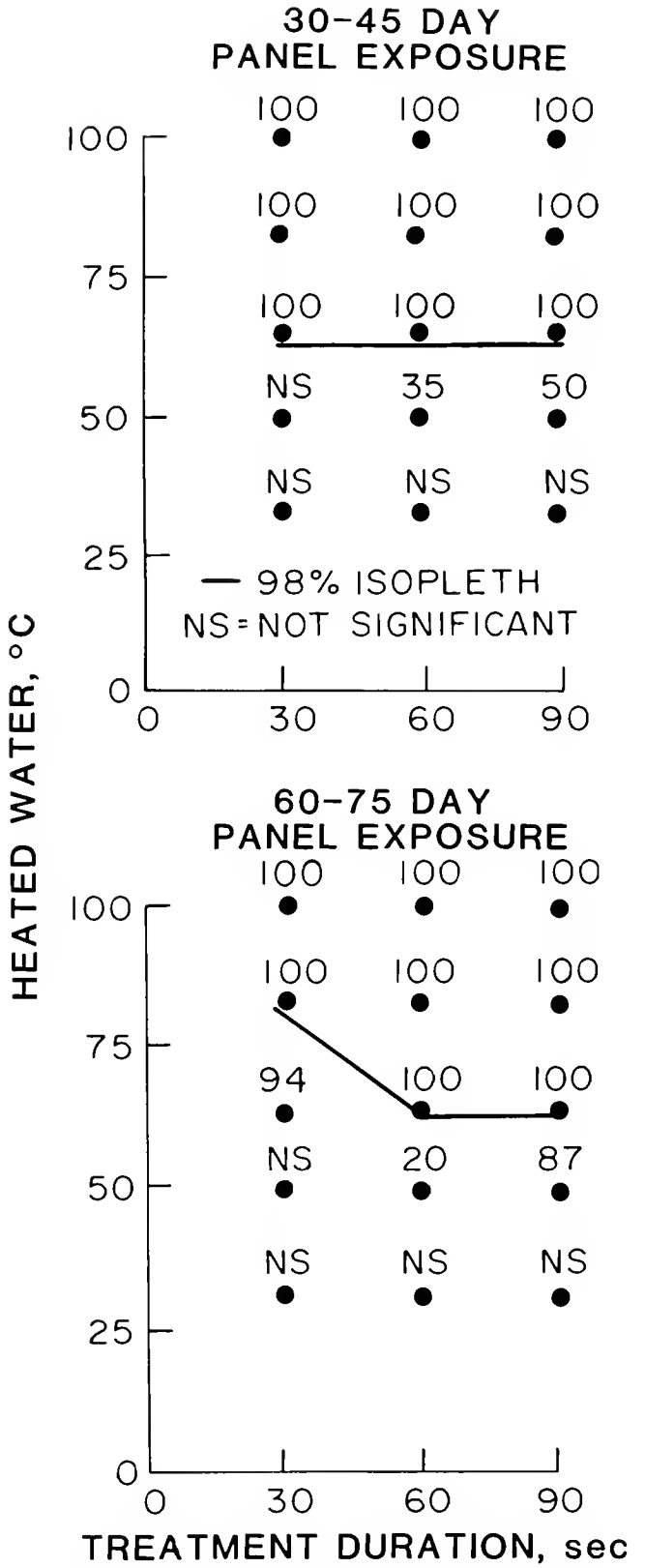

Figure 1. Percent mortality for the heated water treatments.

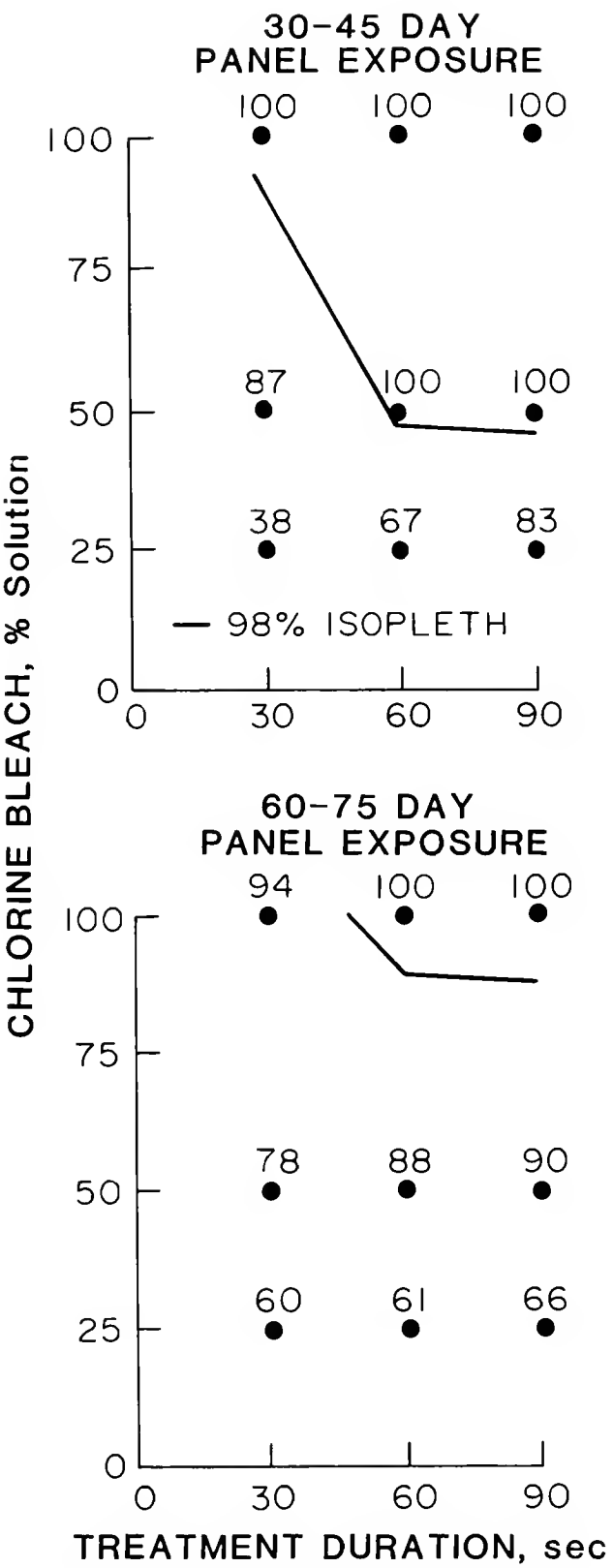

Figure 2. Percent mortality for the chlorine bleach treatments.

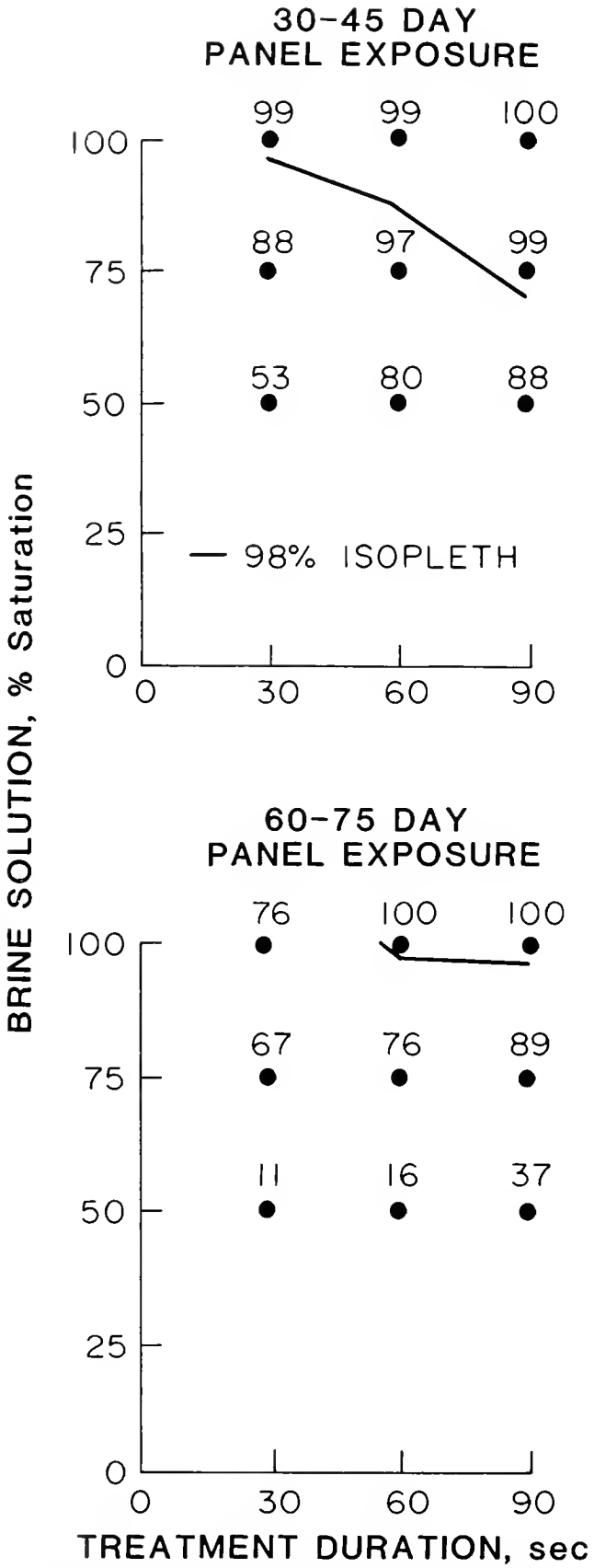

Figure 3. Percent mortality for the brine solution treatments.

A saturated brine solution caused a 99 percent mortality for a treatment duration of 30 sec or longer on animals infested on panels exposed for 30–45 days at sea. Similarly, the saturated brine solution affected a 100 percent mortality for a treatment duration of 60 sec and longer on animals infesting on panels exposed for 60–75 days.

DISCUSSION

The results of the acute toxicological screening of the three treatment methods on *Xylophaga* infested panels exposed for 30–45 and 60–75 days indicate that all three methods were effective under laboratory conditions. Yet, the purpose of the study was to identify a treatment that would be effective as well as practical at sea. Despite the positive results of the laboratory experiments and the assurance of some lobstermen that a heated water dip tank at sea would be a tractable solution to the problem, there are concerns about the safety of this treatment during fishing operations. The chlorine bleach solution proved effective in the laboratory, but also poses safety concerns including splashing on fishermen and causing slippery decks. The saturated brine solution treatment is both effective as a biocide for juvenile *Xylophaga*, and is completely safe and practical on the deck of a fishing vessel. This is the recommended treatment system.

The treatments discussed herein were limited to panels exposed for 30–45 and 60–75 days only. Treatments were evaluated on panels exposed for 90 and 150 days with limited effectiveness because the degree of wood destruction in these older panels was so extensive so as to limit the utility of periodic treatment methods as a viable solution to the problem.

Having identified a simple effective treatment, that is, a 30-sec dip in a saturated brine solution at 30-day intervals, the next phase of the project will be to field test the technique at sea. Small "mini-traps" constructed of red oak lath and ballasted with a traditional brick to insure a negative buoyancy have been offered to lobstermen in the region for treatment evaluation. Each participating fisherman has been provided two experimental "mini-traps". One trap will be dipped at 30-day intervals in the saturated brine solution. The other trap will be handled similarly, but will not be treated and will serve as a control. After six months of treatments, this potential solution to the boring bivalve problem will be critically evaluated. At that time, the effectiveness of the treatment against other biofouling invertebrates will also be appraised although it is anticipated that it will be equally effective due to the general low tolerance of these animals for hypersaline solutions (Kinne 1971).

Concurrent research is being conducted on the distribution, growth, and reproductive biology of *X. atlantica* in an effort to determine seasons and locations of spawning and settlement. This information will further assist the develop-

ment of the proposed treatment system by indicating periods when treatment will be required.

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Support for this project has been provided by the University of Rhode Island Sea Grant Marine Advisory Service, the Department of Zoology, and the Department of Fisheries, Animal and Veterinary Science. The F/V Reliance was lost in November 1987, with all crew aboard while tending traps and collecting our wood panels. We extend our deepest sympathy to the families of the Captain and crew. The encouragement and assistance of R. D. Turner and Captains A. Eagles and P. Bennett is appreciated greatly. This is contribution number 2438 of the University of Rhode Island, College of Resource Development, Agricultural Experiment Station, Kingston, R.I., U.S.A. 02881.

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ASPECTS OF THE BIOLOGY RELATING TO THE FISHERIES MANAGEMENT OF NEW ENGLAND POPULATIONS OF THE WHELKS, *BUSYCOTYPUS CANALICULATUS* AND *BUSYCON CARICA*

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ABSTRACT The impact of fishing pressure on local populations of whelks, *Busycotypus canaliculatus* and *Busycon carica*, was obtained by assessing population density in 1978 and 1981 in Nantucket Sound, Massachusetts. Direct census by SCUBA transects yielded a mean population density for *B. canaliculatus* of 4.80 and 4.06 whelks per 1000 sq. M. in 1978 and 1981, respectively. Subsequent trapping for whelks in the same area in 1978 and 1981 yielded a mean trap catch of 16.54 and 13.88 whelks per trap, respectively. These two independent density estimates are related by a simple model relating population density (D) to trap catch (C): $D = -0.28 + 0.31C$; $r = 0.89$. Potential utilization of this model to estimate the density of *B. canaliculatus* based on commercial catches is discussed. Mean size (shell width) for male and female whelks was obtained for the population of whelks in near shore Nantucket Sound near Cotuit, Massachusetts. Whelks caught by trap and transect were significantly smaller in 1981 compared to 1978. An intensification in the trap fishery for *B. canaliculatus* and the trawl fishery for *B. carica* has occured in southern New England in the last ten years. Catches in the early 1970's approached 681,818 kg (1.5 million lbs.). In subsequent years, the catch per unit of effort for *B. canaliculatus* in Massachusetts and Rhode Island has declined significantly. Current fisheries data on fishing pressure in the southern New England region is presented for both whelks and the need for additional biological information for these snails discussed

KEY WORDS: Population density, growth rate, fisheries management, *Busycotypus*, *Busycon*

INTRODUCTION

The neogastropod whelks, *Busycotypus canaliculatus* (Linne' 1758) and *Busycon carica* (Gmelin 1791), are conspicuous elements of the subtidal fauna of southern New England waters. Occuring from intertidal regions to the continental slope from southern Cape Cod to northern Florida (Johnson 1934, Abbott 1974), whelks of both genera are relatively large, mobile predators on a range of bivalve molluscs (Magelhaus 1948, Paine 1962, Kent 1983). Human utilization of whelks over the last 125 years has been largely limited to pest control as whelks are significant predators on clam and oyster populations in nearshore habitats (Shaw 1960). In addition, there has been a fishery for whelks harvested as by-catch in southern New England for over 100 years (DeKay 1843). In Massachusetts, Rhode Island and eastern Connecticut coastal waters this fishery has provided an economic supplement to specialized fisheries for lobster and finfish, but over the last fifteen years a directed fishery has developed for whelks as interest and the economic viability of the largely ethnic market for whelks has increased.

A trap fishery exists for the channeled whelk, *B. canaliculatus* between May and November. The nature of this fishery is very similar to that of the fishery for American lobster (*Homarus americanus*, Milne-Edwards) in that traps are baited and hauled at regular intervals. In addition to the trap fishery for *B. canaliculatus*, a trawl fishery exists for both *B. canaliculatus* and the knobbed whelk, *B. carica*. Live whelks of both species are generally processed at one of three processing plants in Rhode Island and Massachusetts. In 1981 landings for both genera in southern New England exceeded one million pounds (454,545 kg) of processed meats, up from about 300,000 pounds (136,364 kg) in 1979, as interest in the fishery increased greatly (N.M.F.S. 1986). Landings peaked in 1984 at about 1.4 million pounds (636,364 kg) as the price of processed whelk meats exceeded $1.80/pound, but have declined since. In 1987, landings for the region totalled only 500,000 pounds (227,273 kg) (N.M.F.S. 1986).

In light of the general abundance, and ecological and economic interest in these snails, surprisingly little information pertaining to the biology of these snails in the northern portion of their range is known. As increased interest in the fishery occured in the mid-1970's, several separate investigations were undertaken in Massachusetts (Davis and Matthiessen 1978) and Rhode Island (Sisson 1973, Wood 1979) to assess the extent of the whelk resource in southern New England waters.

This paper will summarize the results of investigations relating to the population density of channeled whelks in Nantucket Sound, Massachusetts. A simple model relating catch to population density is presented for potential use as a management tool in areas where a trap fishery exists for *B. canaliculatus*. In addition, a comprehensive description

of the trap and trawl fishery for whelks is described from the mid-1970's to the present in Massachusetts and Rhode Island.

MATERIALS AND METHODS

Population Density Estimates

The population density of *B. canaliculatus* in Cape Cod near-shore waters was estimated by means of correlating trap catches in various portions of Nantucket Sound with population density estimates as measured by transect sampling using SCUBA divers in 1978, and again in 1981.

Prior to setting traps, the area was sampled by laying a weighted ninety meter line across the seafloor parallel to the prevailing current. Sampling consisted of collecting whelks found within replicate ninety meter long by three meter wide transects established between forty-five and ninety meters apart at depths of 2–5 meters (see Figure 1). Two SCUBA divers were able to effectively sample 270 square meters per transect by collecting whelks on the surface of the substrate as well as those below by physically disrupting the sand and silt bottom to unearth animals completely buried, as well as those buried to the siphon tip. Since *B. canaliculatus* are primarily active at night (Magelhaus 1948), transect sampling was conducted during daylight hours to minimize whelks moving into or out of an area to be sampled. Three to five replicate samples were conducted for each sampling period prior to setting traps in the same area.

Whelk traps consisted of 80 cm × 50 cm × 30 cm high rectangular structures constructed of wood lathes nailed to an oak frame. Whelks entered traps by crawling up the sides and falling through a square opening on top while seeking a bait (dead *Limulus polyphemus,* Linne'). Since *B. canaliculatus* are active nocturnally, traps were baited and set in the late afternoon and picked up the following day. The arrangement of the six trap array on the seafloor was such that the long axis of the rectangular configuration was always perpendicular to prevailing tidal currents (see Figure 1).

Initial calibration of the sampling method involved running SCUBA transects in an area prior to trapping whelks. Density estimates obtained from transect sampling were then correlated with trap catches obtained in the same area over the following twenty-four hour period. Quantitative sampling by SCUBA (three to five replicate 270 sq. meter transects) followed by trap sampling (mean catch of six traps fished for 24 hours) was conducted once per week over a five week period (July–August, 1978) in Nantucket Sound adjacent to Cotuit Bay, Massachusetts. The area sampled is a relatively shallow (1.5–5.0 meters M.L.W.) region characterized by large expanses of sub-tidal sand bars interspersed by deeper troughs containing sand and gravel. Water temperatures varied during the sampling program between 17–20°C. We established transect and trapping sites

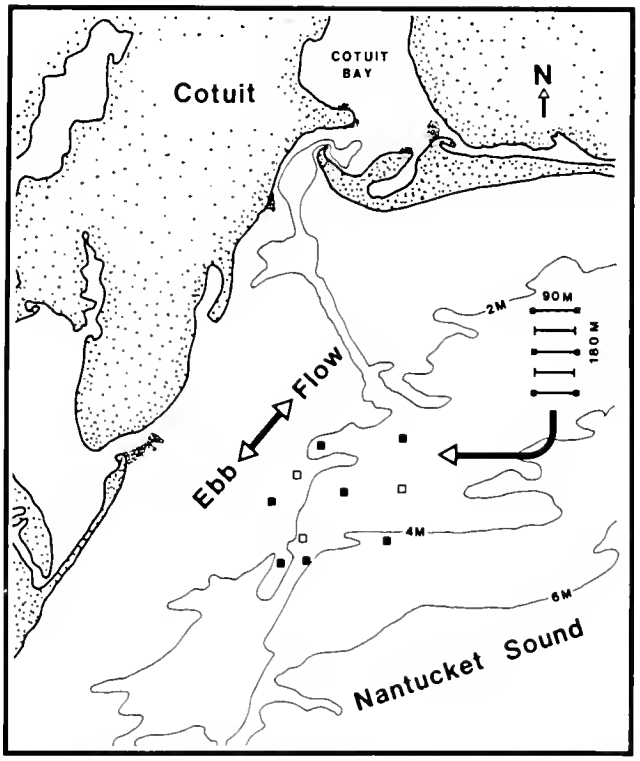

Figure 1. Location of Nantucket Sound site adjacent to Cotuit, Massachusetts. ■ represent 1978 transect and trapping sites □ represent 1981 transect and trapping sites.

for each sample by haphazard placement of the transect line on the bottom within an approximate four square kilometer area in an attempt to sample all the habitats representative of near-shore Nantucket Sound. In no instances did we return to a site that had been sampled previously. Since strong flood (east flowing) and ebb (west flowing) tidal currents in excess of 1.0 knots/hour sweep the area, density measurements were biased in that transects were run parallel to the current, while the six trap array was placed perpendicular to the prevailing tidal currents (see Figure 1 and AREA 1 in Figure 4).

A second series of SCUBA transects followed by trap sampling was conducted in 1981 in the same region to assess changes in population density three years later. The 1981 sampling regime differed from the 1978 sampling protocol in that individual 300 square meter transects (200 meters long by 1.5 meters wide) were run parallel to the current prior to placing a single trap at the mid-point of the transect for a twenty-four hour period.

In order to assess the effective trapping area of whelk traps and therefore the efficiency of a trap to accurately census the adult *B. canaliculatus* population, it was necessary to measure the crawl-rate of channeled whelks. Laboratory trials for crawl-rate were run at the Marine Biological Laboratory in Woods Hole, Massachusetts in August 1981. A three cm layer of beach sand was spread on the

bottom of a water table. Seawater was pumped into one side of the water table at a rate of three liters a minute and exited a standpipe at the far end. Individual whelks for each of eight size classes ranging in shell width from 15–105 cm shell width were placed individually at the upcurrent end. Pulverized razor clam (*Ensis directus* Conrad), a proven stimulent for inciting predatory behavior in whelks (Copeland 1918), was used as an attractant. Drops of this material were added to the water upcurrent from individual whelks; the response was usually immediate in that whelks would extend their siphons and begin to crawl in the direction of the attractant. Sustained crawl-rate trials were run for three individuals within each size class as distance travelled during a four minute trial. Time trials were disregarded in those cases where the whelk stopped crawling during the four minute period.

Whelks caught by trap and transect from Nantucket Sound near Cotuit Bay between June and August 1978 and during August 1981 were measured for morphometric characters. Width measured to the nearest mm. across the aperature with vernier calipers is reported here. Sex was determined for each animal by noting the presence or absence of a penis.

The Whelk Resource and Fishery

The description of the *B. canaliculatus* resource in Nantucket Sound is based on interviews conducted in 1978 and 1981 with whelk fishermen and processors in Massachusetts and Rhode Island. Since the fishery for this resource involved only 30–35 fulltime fishermen, the individuals contacted over the course of this study constituted a significant portion of the people involved in the fishery. Information concerning total annual trap catch and catch per unit of effort was obtained for Nantucket Sound, Massachusetts. In 1988, an additional series of interviews was conducted with two Rhode Island whelk processors in addition to key informants selected from the State of Connecticut Department of Agriculture, State of Massachusetts Division of Marine Fisheries, State of New York Department of Environmental Conservation, and the State of Rhode Island Division of Fish and Wildlife. These interviews form the basis for assessing the present status of whelk stocks in Rhode Island, Connecticut, New York and Massachusetts.

RESULTS

Population Density Estimates

Thirty 270 square meter transects were quantitatively sampled by SCUBA between July 20th and August 25th, 1978 in Nantucket Sound near Cotuit Bay (Figure 1). In 1981, eight additional transects were run on three dates between August 5th and August 26th in the same area. Data acquired for each sampling period includes an estimate of population density obtained by transect sampling. This was followed by a count of whelks caught in traps after twenty-four hours. Results are reported for each sampling date in Table 1 as the mean and standard error. The results of transect followed by trap sampling over seven sampling dates

TABLE 1.

Summary of transect and trapping data for Nantucket Sound in 1978 and 1981.

Date	Transect Area	Catch/Trap	Transect Density	Catch Ratio
20 Jul 78	560	4.92*	1.79	0.36
21 Jul 78	810	23.67	7.41	0.31
30 Jul 78	1350	14.33	4.44	0.31
3 Aug 78	1350	16.00	3.70	0.23
9 Aug 78	1080	20.00	6.48	0.32
17 Aug 78	1350	13.67	4.44	0.32
25 Aug 78	1350	23.22	5.33	0.23
		$\bar{x}$ = 16.54	$\bar{x}$ = 4.80	$\bar{x}$ = 0.30
		S.E. = 2.46	S.E. = 0.70	S.E. = 0.02
5 Aug 81	400	16.00	6.67	0.42
	400	1.00	.00	–
	400	17.00	6.67	0.39
13 Aug 81	600	14.00	3.33	0.24
	600	9.00	1.67	0.19
	600	9.00	1.67	0.19
26 Aug 81	400	15.00	5.00	0.33
	400	30.00	7.50	0.25
		$\bar{x}$ = 13.88	$\bar{x}$ = 4.06	$\bar{x}$ = 0.29
		S.E. = 2.95	S.E. = 0.99	S.E. = 0.03

* Catch adjusted to 24 hour set

in 1978 showed that the density of channeled whelks at this time was less than five whelks per 1000 M^2 (4.80 ± 0.70) while the trap catch averaged greater than sixteen whelks per trap (x = 16.54 ± 2.46). The ratio between channeled whelk density and catch per trap for each sample date was (x = 0.30 ± 0.02), suggesting that population estimates based on trap catches may accurately predict density estimates conducted by direct census. In August 1981, population density based on eight transects sampled on three dates showed a decrease in average density to 4.06(±0.99) whelks per 1000 sq. meters. Trap catches were also depressed at 13.88 ± 2.95 whelks per trap compared to the 1978 sample. The relationship between transect density and trap yield remained intact, however as the catch ratio was 0.29(±0.03) during this sampling period (Table 1). Figure 2 shows these relationships more explicitly as increasing numbers of whelks are caught in traps in areas with higher densities of whelks. Density measurements and mean trap catches are related by the linear regression equation D = −0.28 + 0.31C, where D = predicted population density based on the trap catch (C) fitted by Model II regression (Sokal and Rohlf 1969). The correlation coefficient (r = 0.89) is indicative of the intensity of association between these variables.

Results of crawl-rate trials for individuals in eight size classes are described in Figure 3. All crawl-rate trials were conducted during daylight hours at a seawater temperature of 21–23°C. Maximal crawl rates of 24.9 cm/min. were observed for *B. canaliculatus* in the 85–90 mm shell width size category. Crawl-rates of juveniles and larger animals were significantly less than for the middle size ranges tested.

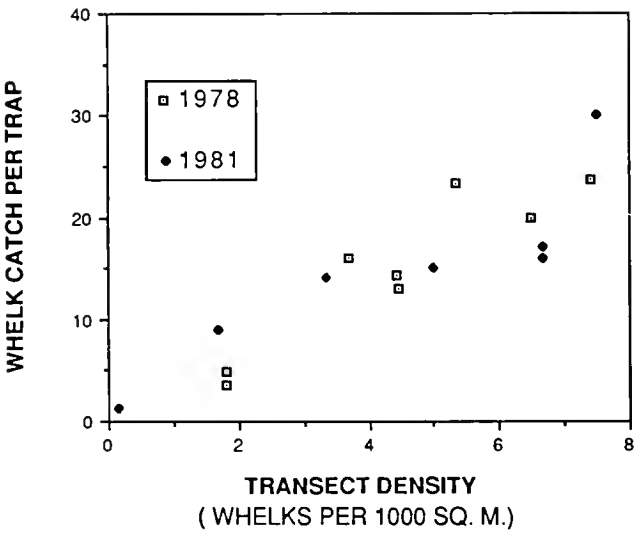

Figure 2. Relationship between trap catch and *B. canaliculatus* population density measured by transect census. ■ represent 1978 samples (N = 7) □ represent 1981 samples (N = 8). The relationship between trap catch and transect density described by the equation D = 0.31 − 0.28C; r = 0.89.

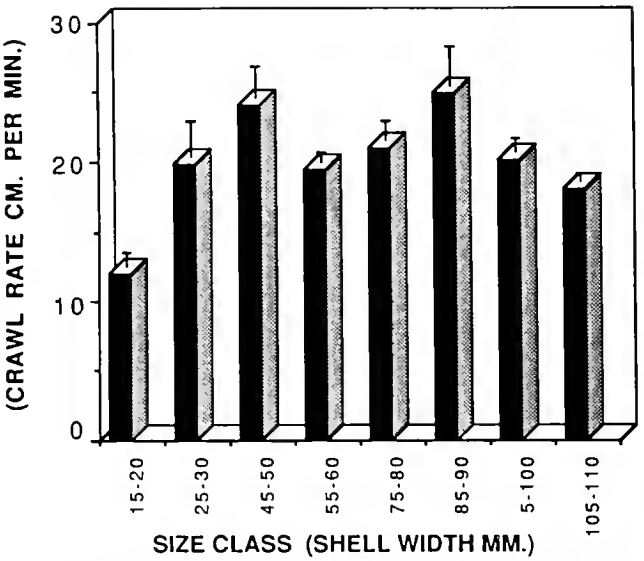

Figure 3. Relationship between size (shell width in mm.) and the rate of locomotion for *B. canaliculatus*. Each bar represents the rate (mean ± standard error) for three individuals in each size class.

There was a significant decline in the mean size of both male and female whelks caught in traps in the Cotuit region between 1978 and 1981 (Table 2). Male *B. canaliculatus* declined about 4% in mean width while female whelks declined 8% in average width. This difference in mean width for both males and females was statistically significant at the 0.05 level (Students T-test; Zar 1974). The sex ratio of females to males of 1:3.7 was the same in 1978 and 1981 for whelks sampled by trap and transect in Nantucket Sound near Cotuit.

Commercial Fishing Pressure in Nantucket Sound

Fishing pressure on the channeled whelk population was assessed based on interviews with several trap fishermen in the Nantucket Sound region. All of the fishermen questioned fished in excess of 100 traps so that this sample constitutes several of the major "players" in the fishery.

Fishermen in this region generally haul traps every second or third day; generally making between 100 and 110 trips per season. The fishing season lasts between early May and mid November. Table 3 describes the major com-

TABLE 2.

Mean size of male and female *B. canaliculatus* from trap and transect sampling in 1978 and 1981.

Year	Male			Female		
	$\bar{x}$	95% C.I.	N	$\bar{x}$	95% C.I.	N
1978	78.75	0.12	148	97.23	1.03	40
1981	75.93	0.12	149	89.43	1.03	41

The difference in mean width (measured in mm.) between years for both males and female whelks is significant at the .05 level; Student T-test.

TABLE 3.

Commercial Trapping in Nantucket Sound.

Site	Year	Traps	Trips Year	Total Lbs.	Lbs./Trap/ Trip
Martha's	1979	100	105	180,000	17.14
Vineyard	1980	125	105	200,000	15.24
	1981	150	105	230,000	14.60
Chatham	1979	125	100*	80,000	6.40
	1980	125	100*	80,000	6.40
	1981	125	100*	80,000	6.40
Hyannis	1977	150	100*	200,000	16.67
	1978	150	100*	200,000	16.00
	1979	150	100*	100,000	7.33

* Approximate number trips per year

ponents of the fishery as it pertains to three individual fishermen operating in different portions of the sound during the years 1977–1981. The informant from Chatham fished an average of 125 traps in the eastern portion of Nantucket Sound at depths averaging nine meters (AREA 2 in Figure 4). This individual averaged a yield of 6.4 pounds (2.91 kg) per trap per trip between 1979 and 1981; totalling 80,000 pounds/year (36,363 kg).

The informant from Martha's Vineyard fished between 100 and 150 traps between 1979 and 1981 in depths averaging 12 meters in AREA 3 (Figure 4). Trap yields averaged 17.14 lbs. (7.79 kg)/trap/trip in 1979. This yield declined to 15.24 lbs. (6.93 kg) in 1980 and 14.6 lbs. (6.64 kg)/trap/trip by 1981. This fisherman caught over 650,000 pounds (295,454 kg) over this three year period. A second informant from Marthas Vinyard fished 90–150 traps in Area 3 as well in 1981 with yields of 11.66 pounds (5.3 kg)/trap/trip.

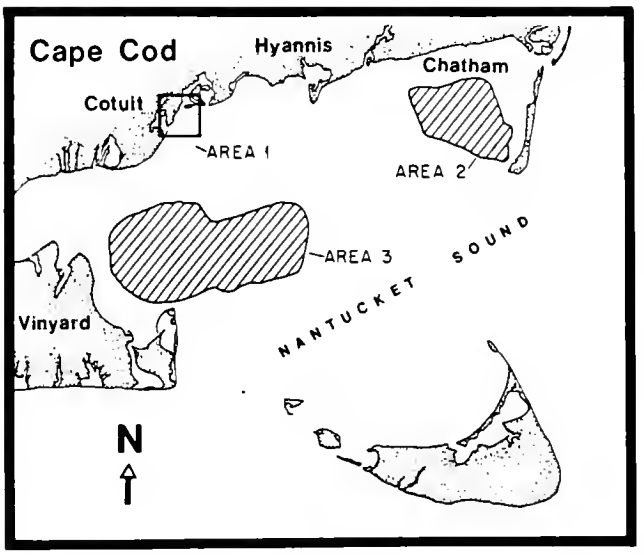

Figure 4. Map showing principle areas fished commercially for *B. canaliculatus* in Nantucket Sound, Massachusetts. Area 1 refers to study site shown in detail in Figure 1.

Finally, the informant from the Hyannis region of Cape Cod fished the area north of AREA 3 (Figure 4). Fishing 100 traps between 1977 and 1979, trap yields declined over this period for this individual from 16.67 pounds/trap/trip in 1977 to 7.33 pounds/trap/trip in 1981. This fisherman caught approximately 500,000 pounds (227,273 kg) of *B. canaliculatus* over this three year period. For all fishermen interviewed, the average mass of a trapped whelk was reported to be approximately 0.5 lb. (1.1 kg) in 1978, 1979 and 1980. The number of individuals involved in the whelk fishery in Nantucket Sound between 1978 and 1981 fishing a hundred or more traps varied between twelve and twenty.

DISCUSSION

The precise estimation of density and related demographic parameters for mobile populations of marine invertebrates represents a major challenge to ecologists and resource managers as commercially important and ecologically sensitive stocks decline due to overfishing, habitat destruction and pollution. Traditional approaches in ecology and fisheries biology have relied on modifications of mark-recapture (MR) sampling programs to estimate population densities (see Pollack 1981 for review), or direct census techniques where estimates are based on counts of individuals within a defined area. There are three critical assumptions to MR and census approaches. The first two require geographic and demographic closure as prerequisites. In addition, equal catchability of the animal in question must be ensured. These are non-trivial assumptions; the first two are frequently impossible to meet in most ecological work (Caughley 1977, Buckland 1982, Begon 1979, 1983). In addition, both approaches are time and resource intensive.

An alternate approach to estimating population density could utilize counts from traps placed in the field for the animal under investigation. Critical to this approach is a means to calibrate the population estimate based on trapping success by obtaining an instantaneous measure of population density from census data. There are few density estimates for animals based on this approach because of the difficulty of obtaining accurate census data by MR or transect sampling for many animals. Population density estimates of marine invertebrates based on trapping success have been made for King crab stocks in the eastern Bering Sea (Merritt et al. 1988), but these estimates are independent of census information obtained from trawl data, and therefore not directly comparable.

The purpose of the present study was to establish a methodology for assessing *B. canaliculatus* population densities based on trap yields of commercial fishermen in Nantucket Sound, Massachusetts. The model whereby the density of trapable whelks (D) is related to the catch of whelks (C) by the relation $D = -0.28 + 0.31C$ ($r = 0.89$) may be applicable to assessing whelk stocks where accurate census data exists for the exploited population.

Transect sampling followed by trapping in 1978 and 1981 in Nantucket Sound yielded similar information with respect to the relationship between measured population densities of adult whelks and the trapability of these animals. We felt confident that all trapable whelks were sampled during SCUBA transects because the substrate (sand and silty sand with some gravel) was easy to manipulate by divers swimming slowly along the transect. Magelhaus (1948) and Kent (1982) mention the difficulty in detecting whelks that had remained stationary in the substrate for some time, and therefore became buried by shifting sand. We attempted to minimize this problem by utilizing the sampling method described above.

The mean catch ratio of approximately 0.30 in 1978 and 0.29 in 1981 (Table 1) indicates that individual traps are drawing on an area of approximately 3333 square meters, irrespective of population density in the area. Laboratory tests of locomotion in *B. canaliculatus* demonstrated that sustained crawl-rates of about 25 cm. per minute are possible for whelks in the size range most frequently trapped (Figure 3 and Table 2). If these crawl rates measured in the laboratory are representative of sustained rates of locomotion in the field (unpublished observations by J.P. Davis suggest that they are), then adult whelks can potentially travel 180 meters in 12 hours, or 360 meters in 24 hours. If distance travelled by individual whelks towards a baited trap occurs over a twelve hour period (the maximum amount of time the current would carry the suspended olfactory attraction in any one direction during ebb or flood tides), it is readily apparent that whelks can easily cover the distance to a trap within a twenty-four hour period if they are less than a couple of hundred meters down-current of the trap. The apparent consistency in measured catch ratios for both years suggests that most whelks within two hundred meters, or an approximate 3300 square meter area, are capable of reaching and are likely to enter a trap within twelve hours, regardless of population density. Catches of whelk after forty-eight hours are not significantly greater than those at twenty-four hours (J. P. Davis, personal observations). This may be due either to consumption of the bait by trapped whelks, or simply to degradation of the bait after one day such that fewer animals are attracted after the first night.

The middle portion of Nantucket Sound between Cape Cod and Martha's Vineyard is a relatively homogeneous region consisting of shallow sandbars (<3 m M.L.W.) and deeper regions (>10 m M.L.W.) characterized by a hard sand-silt substrate (Fogarty 1981). The region supports a significant population of *B. canaliculatus* (Davis and Matthiessen 1978).

Under the assumption that the habitat in the middle portion of Nantucket Sound is similar to that in AREA 1 adjacent to Cotuit (Figure 4), population estimates may be made based on trap catches by commercial whelk fishermen. SCUBA observations of the deeper portions (5–10 m M.L.W.) of Nantucket Sound support this assumption (J. P. Davis, personal observations). An average mass of 0.5 lb. (1.1 kg)/whelk was reported by fishermen in 1978 and 1979 for Nantucket Sound. For AREA 3 (Figure 4), trap catches in 1979 averaged 17.14 lbs. per trap. This represents a mean catch for the informant from Martha's Vineyard fishing this region in 1979 of 34.3 whelks per trap. In 1980 trap catches yielded a mean of 30.48 whelks per trap. Applying the linear regression model to these mean trap catches generates population density estimates in this region of 10.35 and 9.17 trapable whelks per 1000 sq. meters. A similar calculation yields a much lower population density of 3.69 trapable whelks per 1000 sq. meters in the Chatham region in 1979 (AREA 2, Figure 4). The informant fishing the area offshore of Hyannis reported trap yields of 16.00 lbs. (7.27 kg)/trap in 1978 and 7.33 lbs. (3.33 kg)/trap in 1979. These reported landings correspond to population estimates in 1978 and 1979 of 10.06 and 4.26 trapable whelks per 1000 sq. meters, respectively.

Information concerning the mean size of whelks caught in commercial traps in 1980 and 1981 for all regions was not obtained so that there is no basis for utilizing the model in these years. The utility of this simple model clearly depends on accurate catch per unit of effort and data for the mean size of whelks trapped by individual fishermen if information concerning population density of trapable animals is to be obtained.

The *B. canaliculatus* population for a heavily fished area of Narragansett Bay was estimated by Sisson (1972) using the Peterson single census technique (Ricker 1958) under the assumptions of both demographic and geographic closure and equal catchability of marked and unmarked whelks. The number of whelks in the 13.38 sq. km area was estimated at 23428 ± 987. This represents a population density of 10 whelks per 1000 sq. meters. A subsequent study using the same MR methods in an adjacent area of Narragansett Bay utilized by the trap fishery provided similar density estimates for *B. canaliculatus* ranging from 11.49–17.42 whelks per 1000 sq. meters (Wood 1979).

The Fishery in Southern New England (1970–1986)

A fishery for whelks has existed in southern New England for over 100 years (DeKay 1843). Early in the 1900's, landings for Massachusetts were reported to be 20,000 lbs. (9091 kg) valued at $5000.00 (Bowers 1904). In areas devoted to oyster production in Massachusetts, Rhode Island, Connecticut and New York, the harvest of whelks has been considered by the states to be predator control (Shaw 1960). In recent years, an intensification of effort due to increased demand contributed to the dramatic increase in the fishery. Landings in terms of both total processed whelk meats and dollar value are represented in Figure 5. This intensification of effort provided an eco-

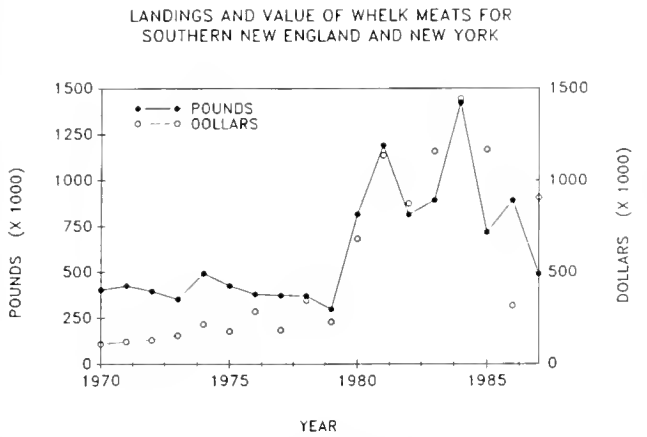

Figure 5. Landings and value of whelk meats processed in southern New England and New York between 1970 and 1987.

nomic boost from landings, processing and distribution of the product to ethnic communities in the northeast region of the United States (Butziger 1968, Amoriggi 1968). Landings and prices peaked simultaneously in 1984 at about 1.4 million lbs. (636,364 kg) and $1.00 per lb., respectively. Both have declined since. In 1987, 500,000 lbs. of processed whelk was caught; this represents a decrease of 65% over three years. In Rhode Island, for example, landings which had averaged 58,000 lbs. (26,364 kg) per year during the early and mid 1960's peaked at 171,000 lbs. (77,727 kg) of whelk meat in 1969. Landings stabilized at about 116,000 lbs. (52,727 kg) of whelk meats in the early 1970's for the New England region (N.M.F.S., Rhode Island Landings 1986). Over the last nine years (1978–1987), Rhode Island landings increased dramatically averaging 223,900 lbs. of whelk meats (101,773 kg) over this time (Figure 5). During this period, ex-vessel prices increased from $0.25/lb. in 1978 to $1.60/lb. in 1987. Massachusetts landings were also very large during this period as well, contributing to the greater than 1.4 million pounds (636,364 kg) yield in 1984 for the region. This represents well over 3.5 million lbs. (1,590,909 kg) of live whelks (N.M.F.S. 1986).

On the basis of conversations with state natural resource personnel from Rhode Island, Massachusetts, Connecticut and New York, it appears that since 1984 the number of fishermen engaged in the trap fishery for *B. canaliculatus* has declined significantly. There is insufficient information to suggest any definitive causes for the decline in interest. Historically, the whelk fishery has been regarded by watermen in the region as a highly seasonal operation; individuals move in and out of the fishery depending on the availability of bait, the ex-vessel price of whelk, and the status of other seasonal fisheries in the region, in particular the lobster and bay scallop (*Argopecten irradians irradians* (Lamarck)) fisheries, as well as seasonal finfisheries for cod, pollock and flounder.

In the last two to three years, most of the fishing effort in Massachusetts is attributed to the trap fishery, although the highest landings are from the trawl fishery in Nantucket Sound, Buzzards Bay, and Vineyard Sound. The trawl fishery targets *B. carica* which is abundant in certain areas (Davis and Matthiessen, 1978). Representative trawls in Nantucket Sound by draggers fishing for groundfish picked up a mean of 1500 lbs. (682 kg)/day in 1978. In 1987, draggers targeting whelks caught an average of 2500 lbs. (1136 kg)/day. Most of this catch was *B. carica* (Anonymous 1988). In addition, during 1987 a small recreational catch was landed in the Cape Cod communities of Harwich, Wareham and Yarmouth (Hickey 1988).

In summary, at present most of the Massachusetts catch can be attributed to approximately twenty trap fishermen, each fishing 150–200 traps, two individuals conducting a directed trawl fishery, and three to five individuals landing whelks as by-catch to directed finfisheries (Hickey 1988).

In Rhode Island ten to fifteen fishermen trap whelk in Narraganset Bay, each fishing approximately 150 traps. At present, there is no directed trawl fishery for whelks by trawlers (Anonymous 1988).

Data from Connecticut (Volk 1988) and New York (Von Volkenburg 1988, Poole 1988) indicates that there is a small but viable trap fishery for *B. canaliculatus* in Long Island Sound, particularly in the mid-sound region near New Haven, CT and around Greenport, NY.

On the basis of correspondance with individual fishermen in the Nantucket Sound region and Narragansett Bay, Rhode Island, trap yields declined dramatically in the central part of both Nantucket Sound and all of Narragansett Bay in 1981 in response to greatly increased fishing pressure. This has continued to the present. Limited data on catch per unit of effort (lbs./trap/trip) for selected Nantucket Sound fishermen (Table 3) suggests that this may be the case, at least in the heavily fished central portion of the region. On the basis of correspondence with one major whelk processor in Rhode Island, catch per unit of effort has significantly decreased in the trap fishery over the last several years. In 1982, this processor received an average of 10–12 lbs. (4.55–5.45 kg.)/trap/day from one client. In 1987, yield per trap for this client was 6.67 lbs. (3.03 kg)/trap/day. In a haphazardly selected sample of 270 *B. canaliculatus* taken in 1988 at a Rhode Island processing plant, a reduction in width of 12–13 mm. was noted relative to a mean width of 75.0 mm reported for the Narragansett Bay region in 1973 (Sisson 1973).

The decline in population density and mean shell widths for both male and female whelks sampled in Nantucket Sound near Cotuit between 1978 and 1981 support the hypothesis that the trapable channeled whelk population has been reduced. Whether this is due to fishing pressure or changes in demographic patterns due to other causes is not known. Information concerning the rate of growth, size at

sexual maturity, fecundity and reproductive effort for northern populations of channeled whelks is needed to address these management issues.

ACKNOWLEDGMENTS

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LATITUDINAL CLINES IN SHELL MORPHOLOGIES OF *BUSYCON CARICA* (GMELIN 1791)

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ABSTRACT Specimens of *Buscycon carica* (Gmelin 1791) were collected from five latitudinally disparate demes along the species range (Wood's Hole, MA, Montauk, NY, Metomkin Bay, VA, Wassaw Sound, GA, St. Mary's Sound, GA). Analysis of variance among and between deme means revealed variation in three specific shell characteristics: spire height, spinosity and shell thickness. ANOVA of the three characteristics revealed significant population differences. The observed morphologic variation closely fits the classic description of a cline. The hypothesized clinal variations are discussed in relation to physical and biological selective pressure gradients found across the species range. Sediment type and predation pressure are believed to be particularly important aspects of the species habitat.

KEY WORDS:

INTRODUCTION

Busycon carica (Gmelin 1791) is a conspicuous gastropod of the estuaries along the east coast of North America from Massachusetts to Florida (Abbott 1974). The species occurs in geographically discrete populations, which show a high degree of variation in shell morphology (Hollister 1958). These dioecious snails pass through trochophore and veliger larval stages within egg capsules and hatch out as fully formed crawling snails. Other gastropods (i.e. *Thais lapillus, T. lamellosa, Littorina saxatilis, Melongena corona*) that have highly localized populations and low dispersal abilities, have been shown to exhibit clinal variation in a variety of shell morphologies (Moore 1936, Kitching et al. 1966, Berry and Crouthers 1968, Kincaid 1957, Spight 1972, James 1968, Janson and Sundberg 1983, Janson and Ward 1984, 1985, Clench and Turner 1956).

The aim of this paper is to present some of the morphologic variations observed in natural populations of *B. carica* and relate them to environmental parameters and clinal variation (Edwards 1985).

METHODS AND MATERIALS

Specimens of *B. carica* were collected from five different localities along the Atlantic coast: Wood's Hole, MA; Montauk, NY: Metomkin Bay, VA: Wassaw Sound, GA; St. Mary's Sound, GA (Figure 1). All specimen shells were weighted (W) on Mettler balances, and the aperture length (AL), shell length (SL), shell width including spines (INW) and width excluding spines (EXW) were measured by metric calipers or a ruler (Figure 2).

These data were used to determine mean and variance of each deme for:

1. Spire height (SH), by using the ratio of shell length to aperture length, which accounts for the age variation in the specimens;
2. Spinosity (SP), by using the ratio of inclusive width to exclusive width;
3. Shell thickness (ST), using the regression line of the power function relating shell weight to shell length ($Y = aX^b$).

Contingency Chi-square tests were used to determine the independence of the morphologic traits and the Chi-square "goodness of fit" test for normality on continuous data was used to determine if the variation within each deme was normally distributed.

Comparisons between demes of shell morphologies ST, SP, and SH were conducted. The ST regression lines were compared using the Bonferroni method, with shell length the independent variable. Analysis of variances (ANOVA) were used to determine differences between deme means for SH and SP. The results of these morphometric tests were used to determine if any latitudinal trends in the data existed.

RESULTS

The five populations had normal variance about their means for the following measurements: SL, AL, INW, EXW based on Chi-square "goodness of fit" tests (Table 1). Spire height is greatest in the northernmost and southernmost populations (Figure 3). Spinosity changes in a N–S direction, with the MA deme having the smallest and the SGA deme having the largest (Figure 4). The measure of shell thickness increased in a N–S direction (Figure 5).

A comparison between populations indicate that significant variation in SH, ST, and SP exist. The ANOVA test on the means for SH had a significant F value (2.7884, df = 4,185). Tests between population means showed that only the NY and VA populations had similar means at the alpha = 0.05 level (Table 2). The ANOVA for SP had a significant F value (68.48, df = 4,165). Tests between population means showed that all but the MA and NY population means were significantly different at the alpha =

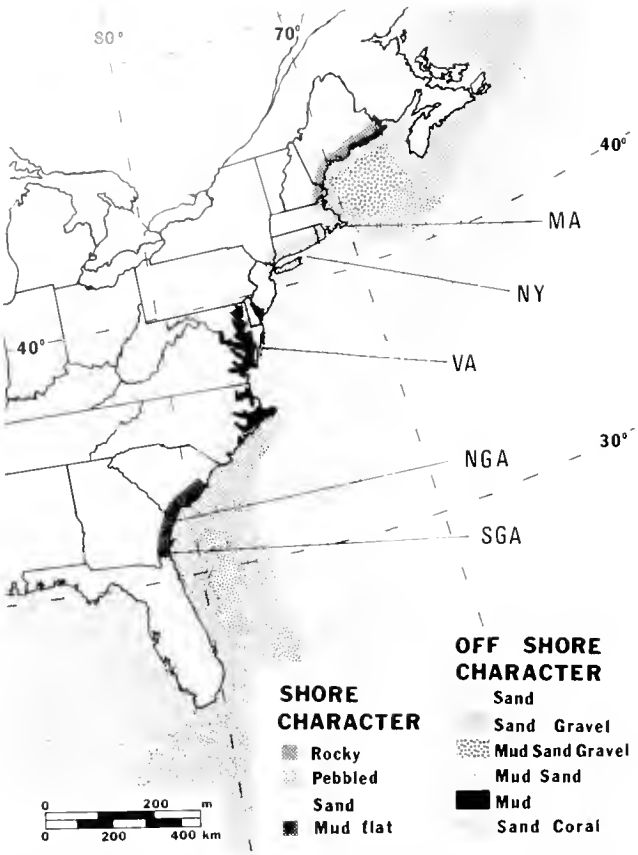

Figure 1. Map of the east coast of North America, showing site locations (MA, NY, VA, NGA, SGA), and sediment characteristics of the shore and offshore zones.

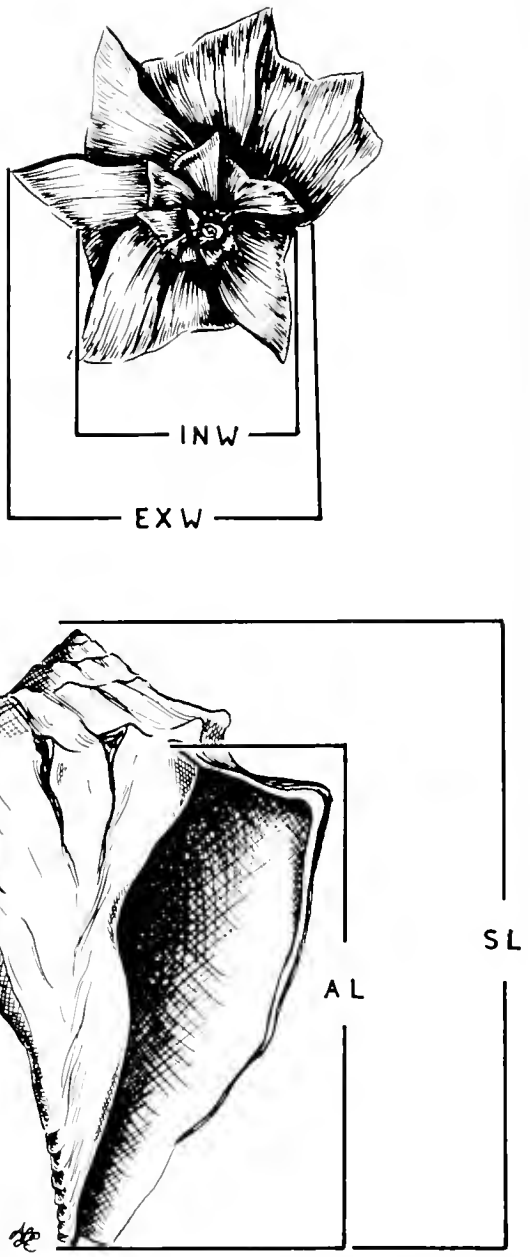

Figure 2. Shell measurements taken: width including spines (INW), width excluding spines (EXW), shell length (SL), aperture length (AL).

0.05 level (Table 2). The F test between ST regression lines was significant (26.28365, df = 8,180). The demes showed minor variations in their intercept values and a general N–S increase in slope (Table 3). Simultaneous comparisons of the slopes (using Bonferroni's method) revealed that the different demes did not have significantly different slopes.

DISCUSSION

The purpose of this study was to determine if measurable morphologic variation occur in latitudinally disparate populations of *B. carica*. Such variations have been related to physical and biological parameters that exert selective pressure across north-south gradients.

Past research has linked clinal variation in spire height and the degree of spinosity to changes in wave exposure (Ballantine 1961, Crouthers 1973, 1974, 1975a, 1975b, 1977, Nayor and Begon 1982), turbulance (Simpson 1985), and the effect of sand scour (Largen 1971, Vermeij and Porter 1971, Vermeij 1973a, 1974). Sand scour is determined by two factors, wave action and substrate consistancy, both of which change latitudinally.

The continental shelf, a determining factor in wave creation, is much wider in the Georgia Bight than farther north. Waves that travel over a shallow basin for long periods of time lose more of their power before they crash upon the shore (Vermeij 1973b). The substrates that populations of *B. carica* encounter in the subtidal estuaries vary from rocky-pebbled, in the north, to silty-sand and silty-clay in the south (USDA 1970, Figure 1). There is a direct relationship between substrate composition and mean particle size. Eighty percent of a pebbled substrate is composed of rock fragments that range in size from 2.0 to 256 mm. Substrates of sand are composed of quartz, felspar and shell particles, 80% of which are between 0.062 and 2.0

TABLE 1.

Means and standard deviations (in parentheses) for each population's shell length (SL), aperture length (AL), inclusive width (INW), exclusive width (EXW), spire height (SH), spinosity (SP), slope constant of the shell thickness regression line (STs), and Y intercept of the shell thickness regression line (STy).

VAR:	SL	AL	INW	EXW	SH	SP	STs	STy
DEME:								
MA	15.11	13.13	3.33	5.80	1.16	1.09	2.70	0.073
	(2.98)	(2.81)	(1.39)	(1.24)	(0.04)	(0.04)	(0.20)	
NY	11.97	10.10	4.82	1.19	1.19	1.07	2.85	0.053
	(1.40)	(1.23)	(0.56)	(0.03)	(0.03)	(0.03)	(0.16)	
VA	21.35	18.14	9.05	8.09	1.18	1.13	3.02	0.040
	(1.92)	(1.53)	(0.67)	(0.66)	(0.03)	(0.04)	(0.09)	
NGA	13.92	11.55	6.97	5.30	1.21	1.31	2.96	0.062
	(2.78)	(2.35)	(1.67)	(1.13)	(0.03)	(0.10)	(0.22)	
SGA	17.92	15.93	9.25	7.31	1.13	1.26	3.03	0.052
	(3.99)	(3.61)	(2.24)	(1.62)	(3.46)	(0.09)	(0.29)	

mm. Clay substrates, such as those found in North and Middle Georgia estuaries, have an 80% particle composition of less than 0.062 mm (USDI 1970, McMaster 1960, Shepard and Cohee 1936, Stetson 1938). The population of *B. carica* from St. Mary's Sound Georgia (SGA), inhabits an estuary that has a significantly lower ratio of silt to clay content than the Wassaw Sound (NGA) deme (SGA: 0.19 to 16.92; NGA: 0.59 to 50.81—Howard and Frey 1975). The difference in particle size between the two estuaries, and therefore the amount of sand scour the two demes experience, may have caused the observed deviation from the clinal trend of SH. The combination of less powerful wave

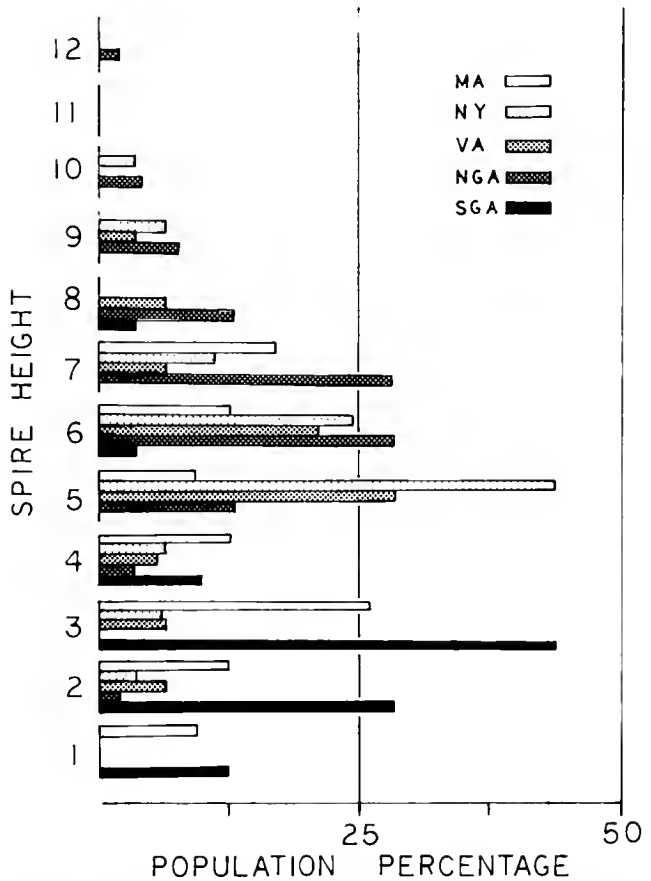

Figure 3. Spire height (SL/AL) as a percentage of the population. Each unit of spire height is equal to 0.02 units of SL/AL, beginning at 1 = 1.09 to 1.11.

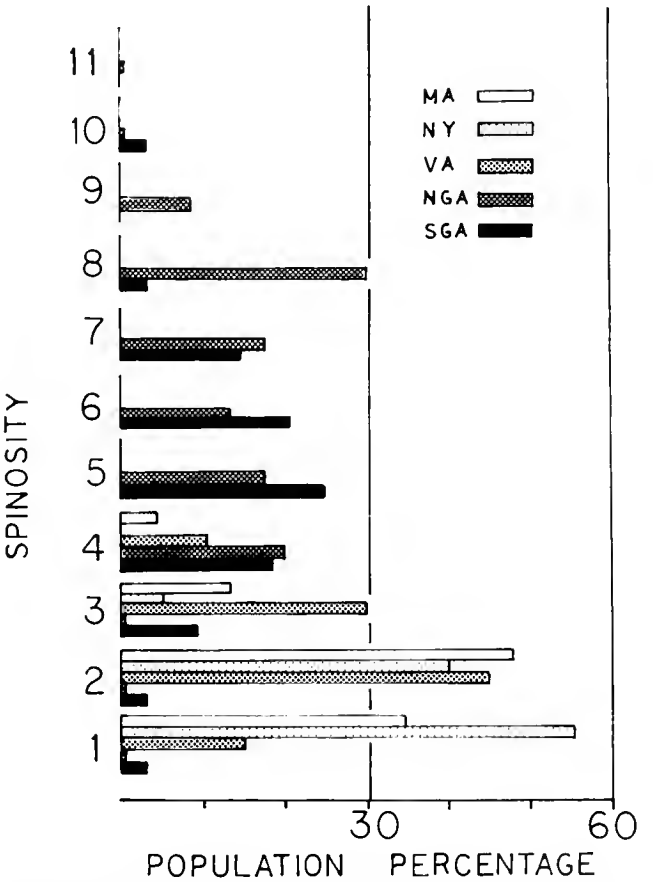

Figure 4. Spinosity (INW/W) as a percentage of the population. Each unit of spinosity is equal to 0.05 units of INW/EXW, beginning at 1 = 1.02.

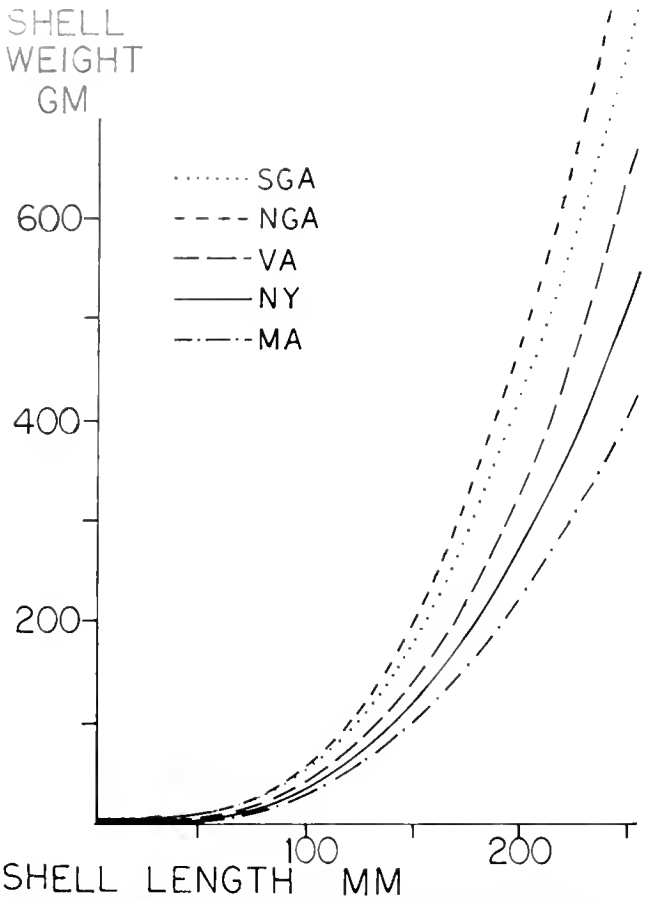

Figure 5. Shell length (SL) vs. shell weight (W), power function regression line ($Y = aX^b$) for each deme. The r^2 for each regression line are: MA = 0.905; NY = 0.814; VA = 0.818; NGA = 0.868; SGA = 0.957.

action and finer sediment particle size reduces the amount of sand scour southern populations of *B. carica* encounter.

In addition to these physical parameters, changes in shell sculpture have been linked to the amount and type of predator populations. Vermeij (1978) suggested that individuals occurring in habitats that have fine substrates can show exaggerations in sculpture that individuals in rocky substrates can not. Low shell sculpture has been tied to the availability of refuges from predators on rocky coasts (*Littorina* sp.—Heller 1976), geometric stability of the shell (may species—Vermeij 1973, *Hysteroconcha* and *Hecuba* —Carter 1967, *Ceratostoma foliatum*—Spight and Lyons 1974), and increasing the size of the penultimate whorl and thus substrate adhesion (Trueman 1983).

TABLE 2.

Z values from between mean tests for spire height (SH) and spinosity (SP).

DEMES	SH	SP
MA-NY	−2.932*	1.825
NY-VA	1.364	−4.250*
VA-NGA	−4.650*	−13.110*
NGA-SGA	11.246*	2.423*

* The null hypothesis, that there is no difference between the two means, is rejected.

The N–S clinal increase in number of mollusc species with shell sculpture and extent of shell sculpture within a species have been related to increases in predation pressure. Predatory crabs and fish populations influenced shell sculpture in comparison between Pacific and Atlantic snails of the same genus (Vermeij 1974, 1976, 1982), between Tertiary and Cretaceous shell types (Vermeij 1977, Stanley 1977), between tropical and temperate snail species (Vermeij 1976, 1978, Vermeij and Currey 1980, Paine 1962, Palmer 1972), and intra species variations of shell thickness (Bergman et al. 1973, Hughes and Elner 1979, Reimchen 1982, VanMarion 1981). The presence of large spines on the shoulders of the shells have been demonstrated to significantly reduce their vulnerability to predation by increasing the effective shell width, reducing the area on which a predator can gain purchase, and directing a predator's exerted force across a broader area of the shell, an area where the shell is thickest (Palmer 1979, Raffaelli 1978, Zisper and Vermeij 1978, 1980). Published data on crabs and fish known to prey upon molluscs show an increase in density and number of species in the southern part of the whelk's range (Vermeij 1977b, 1978).

In addition to a clinal increase in spinosity *B. carica* shows an increase in shell thickness. Increases in shell thickness have been suggested to give only slight increases in shell strength, because resistance to breakage in solids increases as a ⅓ power of thickness (Wainwright et al. 1976, Palmer 1979). Yet clinal changes in shell thickness for species of the family Thaididae have been shown to confer a four-fold increase in resistance to crab crushing (Kitching and Lockwood 1974, Vermeij and Currey 1980). However, even though calcium carbonate is more available to southern populations (Lowenstam 1954a, 1954b, Graus 1974, Vermeij 1978), the cost of producing shell material is prohibitively high, approximately ¼ to ⅓ of the total expenditure for growth (Wilber and Saleuddin 1983). Localized defensive shell thickening (spines) is more energy efficient than an increase in total shell thickness; metabolically it costs less, takes a shorter time to produce, and can confer the same amount of protection at a younger age (Carter 1967, Spight and Lyons 1974, Vermeij 1974, 1978, Palmer 1979).

Whelks inhabit different environments across their latitudinal range and they encounter a variety of physical and biological pressure gradients which combined affect the observed morphology of the animals shells. Each of the demes of *B. carica* investigated in this study exhibited degrees of morphologic variation from the others, while maintaining interpopulation normality. Southern populations displayed increased spinosity and shell thickness, and

decreased spire height. Such variation appears to be common in other recent Busyconinae and across their geologic history (Harasewych 1982). Ernst Mayr (1970) describes a cline as "A gradual and essentially continuous change of character in a series of contiguous populations; a character gradient." Because each character of a population can display clinal variation, the population may belong to several clines. The type of morphologic variation in shell characteristics between demes of *B. carica* can be described as clinal in nature, and related to one or more selective pressures that change across the species north–south range.

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BIOLOGY OF THE RECENT SPECIES OF THE SUBFAMILY BUSYCONINAE

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ABSTRACT The general biology of the subfamily Busyconinae is briefly described. The characteristics of the supraspecific taxa within the subfamily are discussed, and the morphology and biology of their type species described. The current taxonomic arrangement of the Recent species is presented in abbreviated form.

INTRODUCTION

Although never rich in number of species, the subfamily Busyconinae has been a conspicuous component of the marine gastropod fauna of eastern North America through most Cenozoic time. These large marine snails live along the Atlantic and Gulf Coast of North America from Cape Cod, Massachusetts to the Yucatan Peninsula in the waters of the estuaries and inner continental shelf. The subfamily is represented in the fossil record of the area since the Upper Cretaceous (Wade 1917, Emerson 1953, Pulley 1959, Harasewych 1982). Whelks and their egg cases are a conspicuous part of the Recent American coastal fauna. They have been collected, studied, and used as tools and food for well over a thousand years.

For all the animal's prominence and the large body of literature concerning them, many of the most essential components of their biology and evolution remain unknown. This paper presents a brief overview of the life history, distribution and systematics of busyconine whelks, descriptions of the type species of the five currently recognized Recent supraspecific taxa, and an annotated guide to the current taxonomy of the subfamily.

THE BIOLOGY OF BUSYCONINAE

Ovipositing females deposit up to 150 eggs in leathery capsules that are attached to each other at their bases to form a strand. One end of the completed strand, which may contain up to 160 capsules, is buried in the sand to serve as an anchor, while most of the strand is exposed. The capsules that form the anchor, the first to be produced, are misshapen, well separated from each other and contain no embryos. Embryos are not introduced into the capsules until the hormone that causes capsule production has reached elevated levels in the female (Ram et al. 1982). This takes about 15 capsules for *Busycon carica* and 5 capsules for *Busycotypus canaliculatus* (Ram et al. 1982).

The capsules consist of four distinct layers and contain a pre-formed hatching aperture that is sealed by a proteinaceous plug (Harasewych 1978), as in all Muricacea and Buccinacea studied to date (D'Asaro 1988). The fertilized eggs are very large (1 to 2 mm in diameter) and contain large amounts of yolk (Costello et al. 1957, McMurrich 1887). Development is slow, with hatching reported from 100 days (Harasewych 1978) to 13 months (Costello et al. 1957) after oviposition. Cleavage is spiral and shows a transition between holoblastic and meroblastic types (Costello et al. 1957). Metamorphosis, loss of the larval velum, and development of the first postnuclear whorl all occur within the egg capsule prior to hatching. Hatching occurs after a specific proteolytic enzyme dissolves the plug blocking the pre-formed hatching aperture (Harasewych 1978). The young crawl out through this opening as fully functioning snails between 2.5 and 5 mm in length.

Depending upon the species, these snails can reach a length of up to 40 cm. All of the species studied to date are sexually dimorphic with respect to size, females being appreciable larger than the males. This size dimorphism is more pronounced in the genus *Busycon* than in the genus *Busycotypus*. These snails are dioecious, reaching reproductive maturity in 3 to 5 years.

Species of the genus *Busycon* tend to be active at all hours of the day, while the species of *Busycotypus* tend to be nocturnal, at least in intertidal waters (Magalhaes 1948, personal observation). Along the northern portion of the eastern United States, busyconines migrate offshore and into the deeper waters of bays during the winter, as well as during the hotter summer months.

Members of the genus *Busycon* appear to have adapted to prey on venerids and other tightly closing bivalves. These snails are capable of chipping the edges of the bivalve with the lip of their shells until a hole large enough to pass their proboscis through is formed (Clench 1939, Magalhaes 1948). Species of *Busycotypus*, being thinner shelled, prefer to feed on bivalves with gaping valves, and on carrion, although *Busycotypus canaliculatus* has been observed to insert the lip of its shell between the valves of

valves and force them apart until the proboscis can be passed through the gap (Colton 1908). The abundance of *Busycotypus* relative to *Busycon* decreases in the southern portions of their range (Magalhaes 1948), perhaps in response to the decrease in the relative proportion of gaping bivalves.

Busyconine species are distributed across most of their collective ranges in pairs, containing one *Busycon* species and one *Busycotypus* species. Paine (1962) interpreted this as a pairing of species that have different ecological niches and therefore do not compete directly with each other.

In addition to the common, shallow water species upon which the majority of the research has been done, there are a number of deeper water (>100 ft.) taxa about which little is known. These include the three living species of the subgenus *Busycoarctum*, and two subspecies of *Busycotypus* (*Fulguropsis*) *plagosus* all from the Gulf of Mexico, as well as *Busycon* (*Sinistrofulgur*) *laeostoma* Kent from deeper waters off New Jersey, Delaware and Maryland.

The following systematic arrangement of the Recent members of the subfamily largely follows Hollister (1958), but contains subgeneric reassignments and has been updated to include species subsequently described. Hollister's designation of a neotype for *Murex aruanus* Linn, 1758 was inappropriate, and we continue to use the name *carica* (Gmelin 1791) for the type of the genus. For a more comprehensive treatment of the relationships among Recent and fossil busyconines see Harasewych (1982).

SYSTEMATICS OF RECENT SPECIES (TABLE 1)

FAMILY Melongenidae
SUBFAMILY Busyconinae (Finlay and Marwick 1937)
GENUS *Busycon* (Röding 1798)
SUBGENUS *Busycon* (sensu stricto)
TYPE SPECIES *carica* (Gmelin 1791)
TYPE SPECIES

SUBGENUS *Sinistrofulgur* (Hollister 1958)
TYPE SPECIES *sinistrum* (Hollister 1958)
OTHER SPECIES *perversum* (Linné 1758)
pulleyi (Hollister 1958)
laeostomum (Kent 1982)

SUBGENUS *Busycoarctum* (Hollister 1958)
TYPE SPECIES *coarctatum* (Sowerby 1825)
OTHER SPECIES *candelabrum* Lamarck 1816
lyonsi Petuch 1987

GENUS *Busycotypus* (Wenz 1943)
SUBGENUS *Busycotypus* (Wenz 1943)
TYPE SPECIES *canaliculatus* (Linn 1758)

SUBGENUS *Fulguropsis* (Marks 1950)
TYPE SPECIES *spiratus spiratus* (Lamarck 1816)
OTHER SPECIES *spiratus pyruloides* (Say 1822)
plagosus (Conrad 1863)
plagosus galvestonesis (Hollister 1958)
plagosus texanus (Hollister 1958)

SUPRASPECIFIC TAXA AND THEIR TYPE SPECIES

Subfamily Busyconinae (Finlay and Marwick 1937)

General Busyconine characteristics include a large bulbous protoconch of 1+ to 2 whorls, in which the first whorl is equal in diameter to the second. Adult shells of moderate to large size (to 40 cm), subpyriform, with large siphonal canals. Columella with a shallow spiral sulcus near the siphonal fold. Animal with small, squarish foot, large, muscular buccal mass, and long, broad radula with 3–8 cusped rachidian teeth.

Genus Busycon (Röding 1798)

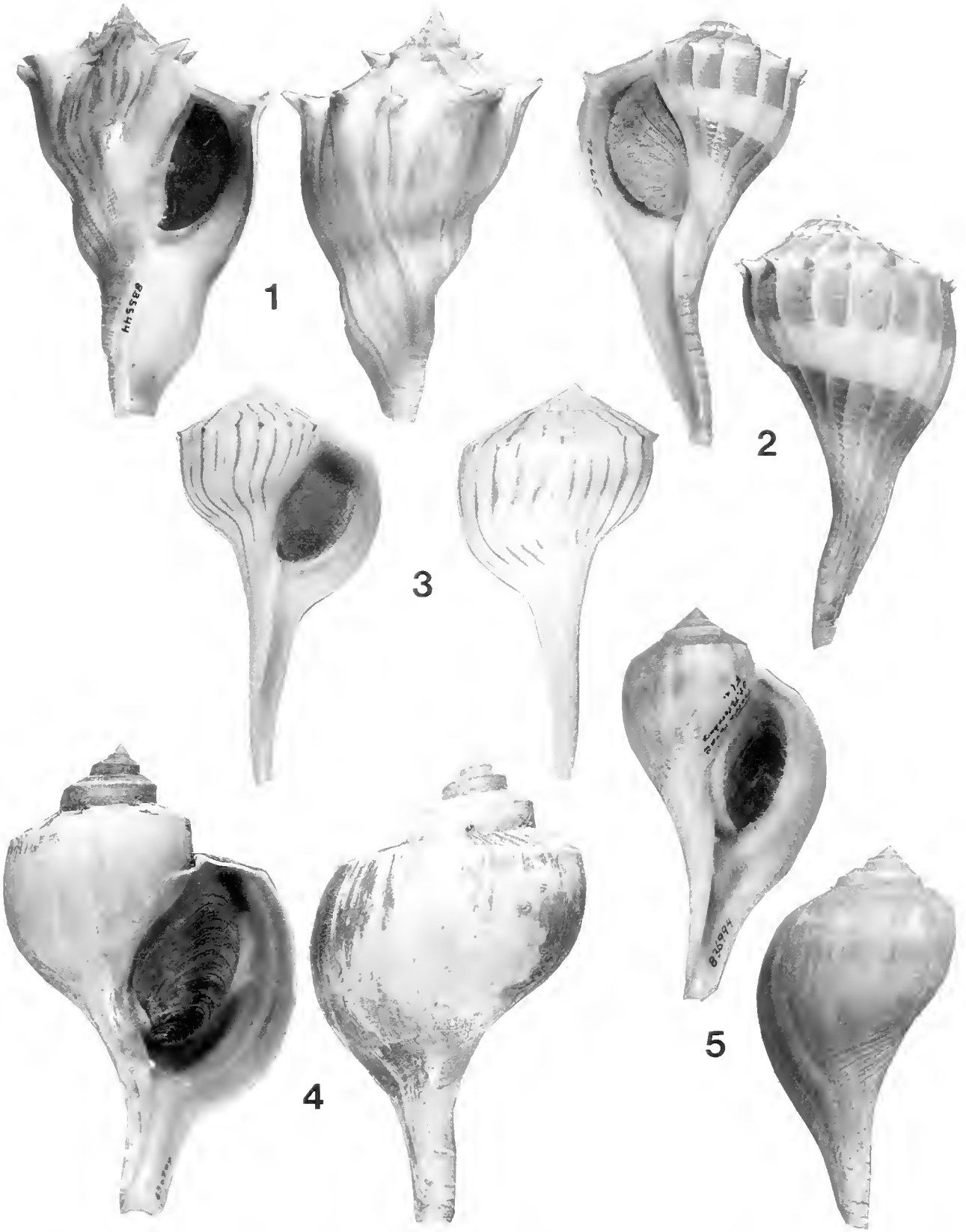
Large, thick-shelled, with tubercles or spines on shoulder. Suture simple, not canaliculate. Shell white to tan in color, often with a lighter band at mid-whorl and darker brown axial streaks. Periostracum fine, low. Exposed portions of animal, including the tentacles, extended proboscis, siphon, and lateral as well as dorsal surfaces of the foot, range from dark gray to black. Rachidian teeth of radula with 4 to 8 cusps.

Type Species: *Busycon (Busycon) carica* (Gmelin 1791), (Figure 1)

Shell large (to 240 mm), dextrally-coiled, heavy, subpyriform, with a low subconical spire. Protoconch of 1+ whorls, teleoconch with up to 8 whorls. Shoulder beaded in early whorls, bears tubercles or spines in subsequent whorls. External color gray to tan, often with dark brown axial streaks, especially in smaller specimens. Aperture color variable, ranging from a very pale yellow, which may or may not be suffused with purple, to a dark deep red.

There is considerable variation in the size and number of spines, aperture coloration and number of denticles on the radular teeth. This species has been divided into the northern subspecies *Busycon carica carica* and a southern subspecies *Busycon* (*Busycon*) *carica eliceans* (Montfort 1810), characterized by thick shell with pronounced spines and a tumid ridge. Recent electrophoretic and morphometric studies (Edwards and Humphrey 1981, Edwards 1985) indicated that subspecific separation of the two morphotypes is unwarranted.

This species ranges from Cape Cod, Massachusetts to Cape Canaveral, Florida. It enters the estuaries to mate and lay egg cases once a year in the north and twice a year in the south.



Figures 1–5. Representatives of the Recent genera and subgenera of Busyconinae. 1. *Busycon* (*Busycon*) *carica* (Gmelin, 1791), *eliceans* morphotype, from off Coco, Florida (USNM 835544), 0.5×. 2. *Busycon* (*Sinistrofulgur*) *sinistrum* Hollister, 1958, off Campeche, Yucatan, Mexico, trawled, (USNM 784635), 0.5×. 3. *Busycon* (*Busycoarctum*) *coarctatum* (Sowerby, 1825), Gulf of Campeche, Yucatan, Mexico [21°30′N, 91°20′W], trawled in 96 ft., (USNM 596714), 0.6×. 4. *Busycotypus* (*Busycotypus*) *canaliculatus* (Linné, 1758), Delaware Bay, Cape Henlopen State Park, Lewes, Delawre, intertidal sand flats, (USNM 836999), 0.5×. 5. *Busycon* (*Fulguropsis*) *spiratum pyruloides* (Say, 1822), Tierra Verde 1sland, St. Petersburg, Florida, subtidal sand flats, (USNM 836994), 0.6×.

Subgenus *Sinistrofulgur* (Hollister 1958)

Characters are the same as in the subgenus *Busycon*, but the shell is sinistrally coiled. Some authors (Grabau 1905, Pulley 1952) considered reversal of coiling to be polyphyletic origin. We consider all Recent left-handed species to share a common, sinistrally-coiled ancestor. The first occurrence of this subgenus dates to the earliest Pliocene.

Type species: *Busycon (Sinistrofulgur) sinistrum* (Hollister 1958), (Figure 2)

Shell very large (to 375 mm), sinistrally-coiled, heavy, subpyriform, with a low subconical spire. Shoulders of the whorls smooth, rounded, or with prominent tubercles or spines. External shell color of small specimens light tan to medium brown, with white band around the mid-whorl, with dark brown axial streaks; larger specimens often gray to pure whilte. Aperture color white to cream.

There is considerable variation in such shell characters as spire height, presence, size and number of shoulder spines, presence of a tumid ridge, and number of denticles on the radular teeth. This has resulted in several species of Recent left-handed whelks being described. Varying opinions regarding the validity of these species have resulted in nomenclatoral instability in the taxonomy of *Sinistrofulgur*. Linné was the first to formally describe a species of left-handed whelk, proposing the taxon *Murex perversus* in 1758 for the heavy-shelled species with a pronounced tumid ridge across the siphonal canal that is restricted to deeper waters off the Yucatan peninsula. Although the taxon *contrarium* was proposed by Conrad (1840) for a fossil species from North Carolina, Smith (1959) and subsequent workers applied this name to the common left-handed whelk. Hollister (1958) correctly recognized the Recent species to be different from the Pliocene *B. contrarium*, and redescribed it as *B. sinistrum*, making it the type species of the subgenus *Sinistrofulgur*. In the same publication, he also described *B.* (*Sinistrofulgur*) *aspinosum*, a round shouldered, spineless ecophenotypic variant of *B. sinistrum*, and *B.* (*S.*) *pulleyi*, a higher spired form from the western Gulf of Mexico. Most recently, Kent (1982) proposed the name *Busycon* (*Sinistrofulgur*) *laeostoma* for a large, offshore species that ranges from New Jersey to Maryland. Although further work is necessary to clarify the relationships between these taxa, the name *sinistrum* has priority for the common-left handed whelk, so long as it is considered to be different from *perversum*. Should the opinion that there is only one living species of left-handed whelk prove to be correct, than the name *perversum* would have priority.

As restricted by Hollister (1958), this species ranges from Cape Hatteras southward to the Florida Keys, then northward to Mobile Bay. It also occurs along the Yucatan Peninsula. It enters the estuaries to mate and lay egg cases once a year in the north and twice a year in the south.

Subgenus *Busycoarctum* (Hollister 1958)

This subgenus, restricted to the deeper waters (>100 ft.) of the Gulf on Mexico in the Recent fauna, is recognized by its heavy, dextrally-coiled, low-spired shell that has prominent apertural lirae.

Type species: *Busycon (Busycoarctum) coarctatum* (Sowerby 1825), (Figure 3)

Shell of moderate size (to 175 mm), dextrally-coiled, heavy, subpyriform, with a low subconical spire and bulbous body. Shoulders with prominent tubercles to short spines. External shell color white to tan, with strong to weak fine, brown axial streaks. Aperture ranges from while to yellow. This species occurs in the Bay of Campeche, Mexico. Until its rediscovery by Clench (1951), it was considered "lost" and possibly extinct. Therefore, it is not surprising that there is no literature dealing with any aspect of its biology.

***Genus Busycotypus* (Wenz 1943)**

Shell large, dextrally-coiled, thin, with pronounced sutural canal. Shoulder smooth or with tubercles. Shell white to deep brown in color. Periostracum hirsute. Exposed portions of animal, including the tentacles, extended proboscis, siphon, and lateral as well as dorsal surfaces of the foot are a mottled gray. Rachidian teeth of radula with 3 cusps.

Type species: *Busycotypus (Busycotypus) canaliculatus* (Linné 1758), (Figure 4)

Shell large (to 200 mm), thin, subpyriform, with a turreted spire. Protoconch of 1+ whorls, teleoconch to 7 whorls. Shoulder tabled, with low tubercles along the periphery. External color from white to dark tan. Aperture without any spiral lirae. Aperture color ranges from white to dark chocolate brown. Suture with deep, U-shaped channel. Periostracum of long hairs. Rachidian teeth of radula with three cusps condensed within the central third of the tooth.

Specimens from the southern portion of the range are less globose and lighter in color, occasionally with pure white shells.

This species ranges form Cape Cod, Massachusetts where it is the most common busyconine species, to Cape Canaveral, Florida, where it is subtidal and uncommon. *Busycotypus canaliculatus* enters the estuaries to mate and lay egg cases once a year.

Subgenus *Fulguropsis* Marks, 1950

Shell dextrally-coiled, pyriform, with rounded shoulder that lacks spine or tubercles. Suture with V-shaped channel. Aperture with numerous spiral lirae ending just within the lip.

TABLE 1.

Shell lengths of Recent species of Busyconinae reported by various authors

Species	Author	Length (cm)	Locality
carica	Dall, 1889	20.0	
	DeKay, 1843	20.32	NY
	Magalhaes, 1948	24.0	NC
	Hollister, 1958	36.4	SC
	Abbott, 1974	22.86	
	Walker, pers. comm.	22.0	GA
	Weinheimer, 1982	18.9	SC
	DiCosimo, 1986	25.0	VA
sinistrum	Dall, 1889	25.0	
	Magalhaes, 1948	26.0	NC
	Hollister, 1958	36.4	SC
	Abbott, 1974	40.64	
	Walker, pers. comm.	21.8	GA
	DiCosimo, 1986	27.6	VA
coarctatum	Clench, 1951	13.8	
	Abbott, 1974	12.70	
canaliculatus	Dall, 1889	25.0	
	Gould, 1841	17.78	MA
	DeKay, 1843	15.24	NY
	Magalhaes, 1948	16.3	NC
	Abbott, 1974	19.05	
	Walker, pers. comm.	13.8	GA
	DiCosimo, 1986	20.0 cm	VA
Spiratus pyruloides	Abbott, 1974	15.24	

Type species: *Busycotypus (Fulguropsis) spiratus spiratus* (Lamarck 1816)

The nominate subspecies is restricted in distribution to the Yucatan Peninsula. The subspecies *pyruloides*, described below, ranges from North Carolina to Mobile Bay, Alabama.

Busycotypus (Fulguropsis) spiratus pyruloides (Say 1822), (Figure 5)

Shell of moderate size (to 158 mm), subpyriform, with a slightly turreted to compressed spire. Shoulders rounded, sutural canal V-shaped. External color white to light tan, with brown axial streaks, generally confined to bands. The aperture of the shell ranges from a whitish-tan to an orange-brown. Shell sculpture of numerous fine spiral threads is most pronounced along the shoulder and siphonal canal.

This species ranges from Cape Hatteras, North Carolina to the Florida Keys, and northward to the Florida Panhandle. It enters the estuaries to mate and lay egg cases twice a year.

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OBSERVATIONS ON INTERTIDAL WHELK (*BUSYCON* AND *BUSYCOTYPUS*) POPULATIONS IN WASSAW SOUND, GEORGIA

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ABSTRACT Two species of *Busycon* and two species of *Busycotypus* occur in the coastal waters of Georgia: the Knobbed Whelk, *Busycon carica*, and the Lightning Whelk, *Busycon contrarium*, in intertidal to subtidal areas; the Channeled Whelk, *Busycotypus canaliculatus*, occasionally intertidally, but primarily subtidally; and the Pear Whelk, *Busycotypus spiratus*, subtidally. At the mouth of the Wassaw Sound, Georgia, *B. carica* accounted for 79%, *B. contrarium* 21% and *B. canaliculatus* <1% of the total number (N = 1191) of intertidal whelks sampled. *B. carica* migrates higher up into the intertidal zone than does *B. contrarium*. *B. canaliculatus* only occurs intertidally on low spring tides. Whelks were on intertidal flats where oysters and clams occur in fall and spring and were in low numbers in winter and summer. A low percentage (8%) of whelks were found actively feeding. Of these, 54% were consuming *Mercenaria mercenaria* and 46% were consuming *Crassostrea virginica*. Of 195 *B. carica* sexed, females outnumbered males 11 to 1 and were larger in shell length (14.8 ± 3.3 cm) than males (10.9 ± 2.8 cm). No males were found among the 57 *B. contrarium* sampled. Of 24 *B. canaliculatus* sexed, females outnumbered males 7 to 1 and were larger in shell length (13.5 ± 2.0 cm) than males (8.2 ± 1.1 cm). The results of this study are discussed in terms of the whelk fishery in Georgia.

KEY WORDS: Whelks, intertidal, populations, migration, fishery

INTRODUCTION

Traditionally in Georgia, the American Oyster, *Crassostrea virginica* (Gmelin) has constituted the dominant species of the molluscan fishery. At times oysters were the only molluscan species being harvested in the coastal waters of Georgia. Today four molluscan species, hard clams, *Mercenaria mercenaria* (L.), Calico Scallops, *Argopecten gibbus* (L.), oysters and whelks, comprise the molluscan fishery in Georgia. The whelk fishery became the dominant (in terms of pounds of meat landed and in dockside value) molluscan fishery in 1982 (Georgia Department of Natural Resources). Whelks are harvested mainly by modified shrimp nets dragged behind shrimp boats in the nearshore areas and are shipped to northern markets where they are sold as "conchs".

Four species of whelks, the Knobbed Whelk, *Busycon carica* (Gmelin), the Lightning Whelk, *Busycon contrarium* (Conrad), the Channeled Whelk, *Busycotypus canaliculatus* (L.), and the Pear Whelk, *Busycotypus spriratus* (Lamarck), occur within the coastal waters of Georgia (Abbott 1974). Considering the commercial importance of whelks in Georgia, it is surprising that little is known about the ecology of the animal in the coastal waters of Georgia. Walker et al. (1980) noted the importance of whelks as predators upon commercial hard clams as well as describing their distribution within Wassaw Sound, Georgia. Edwards and Humphrey (1982) and Edwards (1985) using electrophoretic techniques determined that *Busycon eliceans* was not a true species, but was an ecological form of *Busycon carica*.

Due to the recent importance of whelks to the Georgia fisherman and the lack of basic ecological information pertaining to whelks in Georgia, the distribution, abundance, migration and feeding patterns of intertidal whelk populations in Wassaw Sound, Georgia are reported herein.

METHODOLOGY

Intertidal distribution of whelks was determined by direct observations in intertidal areas about Wassaw Sound, Georgia. At each survey site, whelks were collected, identified to species, notes recorded on their habitat and then released.

Observations were made seasonally at the southern end of Cabbage Island and Dead Man Hammock area of Wassaw Island and monthly at a whelk population at the northern end of Cabbage Island from November 1978 to July 1980. Whelks wre collected from defined areas (7442 m^2, 836 m^2 and 4905 m^2 respectively) at each site, identified to species, counted and their shell heights (i.e., shell apex to the end of the siphonal canal) determined to the nearest mm with vernier calipers. Numbers and species of whelks found feeding and their prey type were recorded at each site. All whelks were returned to approximately their original collection site.

Whelk migration was studied by individually marking whelks (N = 371) with labelled aluminum strips. After transporting whelks to the laboratory, a 10 mm hole was drilled through the shoulder of the shell at the base of the newest spine and approximately 5 mm from the lip, a labelled aluminum strip inserted through the hole and

wrapped around the lip of the shell and the ends cemented together with 5 minute epoxy. Tagged whelks, 139, 93 and 139 were released at the northern and southern ends of Cabbage Island and Wassaw Island respectively.

RESULTS

Whelks were found throughout Wassaw Sound, Georgia (Figure 1) occurring primarily along creek banks or intertidal flats where oysters and/or hard clams inhabited.

The overall species composition of whelks from the three intertidal flats of Wassaw Sound studied from November 1978 to June 1980 was 79% *B. carica*, 21% *B. contrarium*, <1% *B. canaliculatus*, and no *B. spiratus* (N = 1191); however, the species composition varied from a high of 98% *B. carica* at the Wassaw Island site to a low of 63% *B. carica* on the northern end of Cabbage Island. The overall whelk population at Wassaw Island was 98% *B. carica*, 2% *B. contrarium*, and <1% *B. canaliculatus;* for the southern end of Cabbage 86% *B. carica*, 12% *B. contrarium*, and 2% *B. canaliculatus;* and for the northern end of Cabbage Island 63% *B. carcia*, 37% *B. contrarium*, and no *B. canaliculatus*.

Whelk density on intertidal flats was highest in fall and lowest in winter at all three stations. The Wassaw Island densities were higher than those observed at the northern or southern end of Cabbage Island. A density of 778 whelks/hectare occurred on Wassaw Island compared to 139 and 79 whelks/hectare at the southern end and northern end of Cabbage respectively in the fall 1979. Low densities at Wassaw, southern end and northern ends of Cabbage (96, 18 and 3 whelks/hectare respectively) occurred during winter.

Whelks exhibited a similar zonation pattern at the three stations sampled: *B. carica* occurred from subtidal areas to

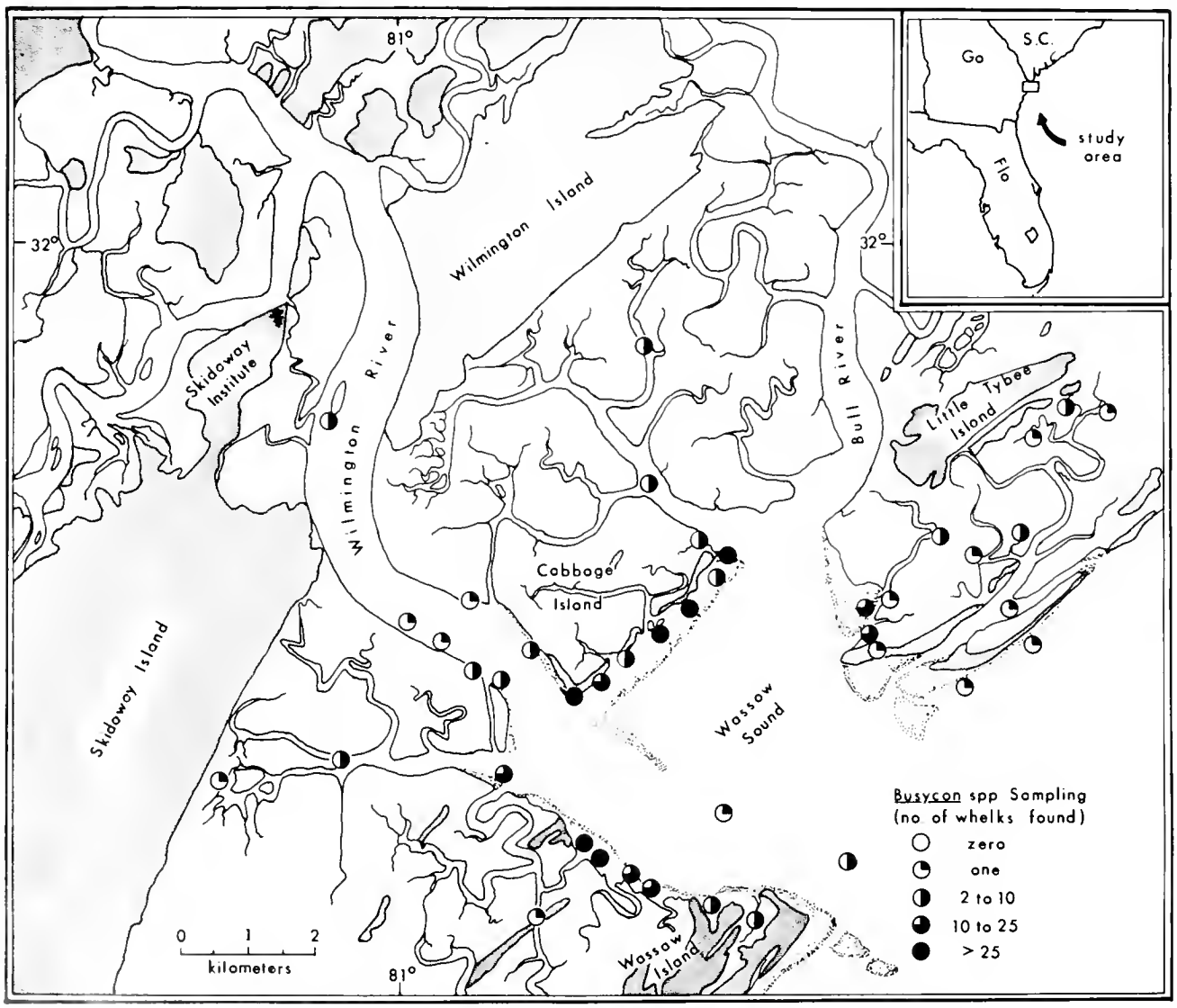

Figure 1. Distribution of whelks (*Busycon* and *Busycotypus*) in Wassaw Sound, Georgia.

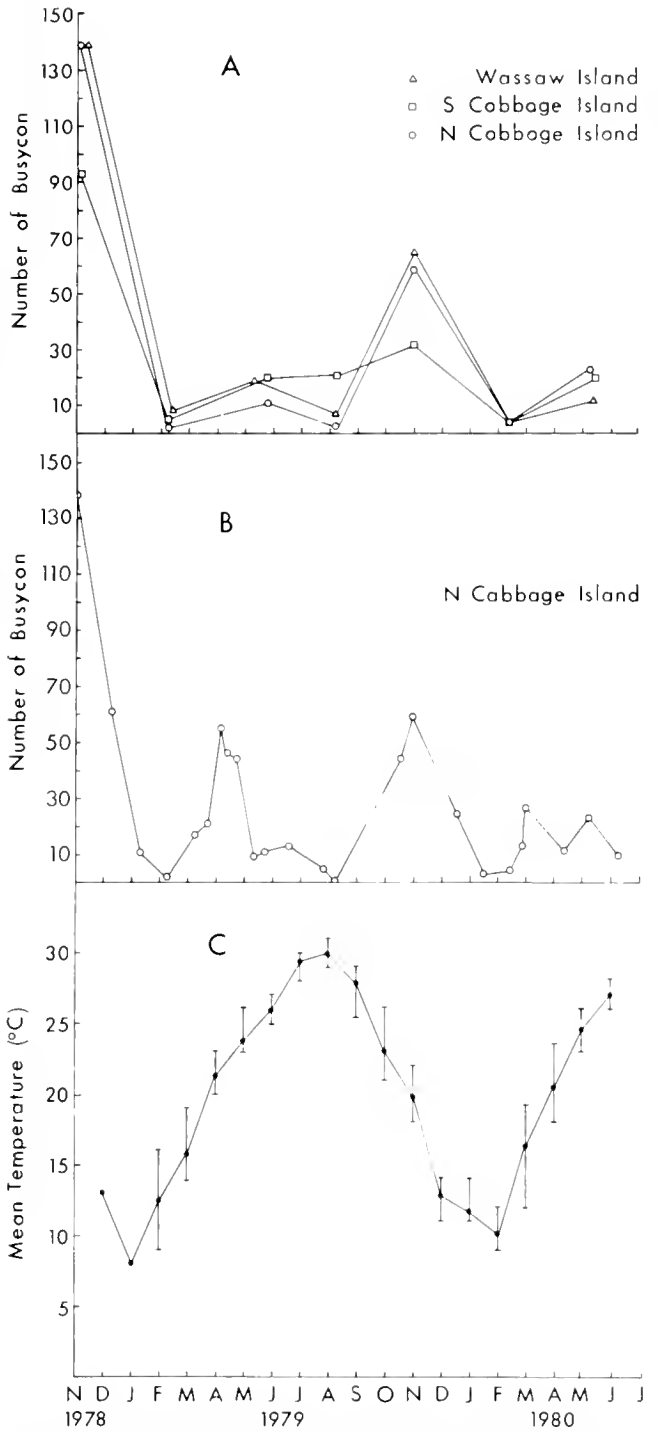

Figure 2. (A) Seasonal counts of whelks from the northern and southern ends of Cabbage Island and Wassaw Island stations, (B) monthly counts of whelks for the northern end of Cabbage Island and (C) seasonal water temperature changes in Wassaw Sound, Georgia.

above the mean neap low water mark; *B. contrarium* occurred from subtidal areas to mean low water mark and *B. canaliculatus* occurred occasionally at the southern end of Cabbage and Wassaw Islands on mean low spring tides. *B. spiratus* was not found intertidally in Wassaw Sound.

Whelks migrate from intertidal flats to subtidal areas and along the tidal flats. Both types of migration were observed at the three stations. Whelks were more abundant on intertidal flats in the fall, in low numbers in winter, abundant in spring, and were low in numbers in summer (Figure 2a and b). When the numbers of whelks are low, the air and water temperatures were at either their maximum or minimum (Figure 2c). Whelks also were observed to migrate between shellfish beds. Tagged whelks on the northern end of Cabbage moved towards the south. *B. carica* (N = 4) were found 600 meters south of the release site in April 1979, with three different *B. carica* being found there in April 1980. Tagged whelks from the southern end of Cabbage tended to follow the current heading north. On Wassaw Island, the whelks migrated westward, following the contour of the oyster bed. A *B. carica* was found 400 meters east of the release site in October 1979. In all cases of recapture, whelks moved from one shellfish bed to another.

Overall the number of tagged whelks recaptured was small as it has been observed in other whelk tagging studies (Magalhaes 1948, Menzel and Nichy 1958, Paine 1962). On Wassaw Island, 34 out of 139 tagged whelks were recaptured, of which three were collected three separate times and six were found dead. From the southern end of Cabbage Island, 21 out of 93 tagged whelks were recaptured, of which three were recaptured a second time and one was found dead. The northern end of Cabbage Island returned 50 out of 139 tagged whelks with 10 recaptured three times, one collected five times and six found dead.

Of 1318 whelks collected, 8% were found preying on oysters and/or hard clams. Of these, 46% were consuming oysters and 54% consuming hard clams. Prey selection per study site is given in Table 1.

Female *B. carica* outnumbered males 11 to 1 (N = 195). Females obtained a greater height (14.8 ± 3.3 cm) than males (10.9 ± 3.0 cm) with females ranging in height from 7.3 to 22.0 cm and males ranging from 6.5 to 17.0 cm (Table 2). No males were found among the 57 *B. contrarium* collected. The sample size of *B. canaliculatus* (N = 24) was too small for adequate analysis. For the six pairs of mating *B. carica* found in March 1980, males averaged 9.4 ± 0.9 cm with females averaging 17.4 ± 1.4 cm in shell height.

DISCUSSION

The seasonal migration pattern of whelks moving onto and off of intertidal flats in Wassaw Sound agrees with observations of Paine (1963) and Kent (1983), but differs slightly from observations made by Magalhaes (1948). The occurrence of whelks in Florida (Paine 1963) peaked in fall and spring and were low in winter and summer. Kent (1983) observed that whelks migrated to subtidal areas during summer with whelks moving into the shallower areas during spring and fall. He did not collect during winter months. In North Carolina, Magalhaes (1948) found

TABLE 1.

Frequency of prey selection by whelks upon oysters, *Crassostrea virginica*, and hard clams, *Mercenaria mercenaria*, at the three study sites.

Station	Total No. Whelks Collected	No. Feeding on Oysters	No. Feeding on Clams
Wassaw Island	299	14	1
Southern end of Cabbage Island	340	22	12
Northern end of Cabbage Island	679	14	45
TOTAL	1318	50	58

that densities of whelks peaked in summer, with half as many whelks occurring in spring and fall as summer. Whelks were not found during winter in North Carolina (see Table 3).

Differences in whelk densities between study sites might be related to densities of the clams and oysters on which they prey (Carriker 1949, 1951) (Table 4). The Wassaw Island station has a large oyster (covering *ca.* 418 m^2) and a low clam (<1 m^{-2}) populations. Southern end of Cabbage Island has several small oyster bars (totaling *ca.* 300 m^2) with an average of two clams m^{-2}. Oysters on the northern end of Cabbage Island cover an area of approximately 625 m^{-2} with an average density of four clams m^{-2}, but clam densities may reach as high as 100 m^{-2} in shelly areas. Oysters cover 50% of the Wassaw Island site, 14% of the southern end of Cabbage Island site, and 8% of the northern end of Cabbage Island study area. As expected from the distribution of clams and oysters, whelks predated primarily on oysters at the Wassaw Island station and primarily on clams at the northern end of Cabbage Island.

Thicker-shelled whelks occurred higher up into the intertidal area than thinner-shelled whelks with *B. carica* occurring farther up than did *B. contrarium*. *Busycon carica* and *B. contrarium* are thick-shelled (4 mm) species while *Busycotypus canaliculatus* and *B. spiratus* are thin-shelled (2 mm) snails (Magalhaes 1948, Paine 1962). *B. carica* and *B. contrarium* are able to prey upon thick shell bivalves, whereas *B. canaliculatus* and *B. spiratus* are not (Paine 1962). Whelks prey on thick shelled clams by using their shell margin to chip away the shell margin of the bivalve. When a hole large enough to allow entry of the whelk shell lip between the clam's valves is formed, the clam is wedged open (Magalhaes 1948). Hard clams and oysters, both thick-shelled bivalves, occur intertidally in Georgia.

B. spiratus is nocturnal (Paine 1962), and *B. canaliculatus* is nocturnal during warmer months (Magalhaes 1948) causing their absence or low occurrence on intertidal flats in Georgia, since sampling occurred only during daylight hours in this study. *B. canaliculatus* is nocturnal during warmer months, feeds both day and night in spring and fall, and feeds during the day in winter (Magalhaes 1948). *B. canaliculatus* occurred in the fall of 1979 at the southern end of Cabbage (N = 3) and Wassaw (N = 1) Islands. *B. spiratus* was not found on intertidal flats during daylight samplings. *B. canaliculatus* is common in subtidal areas of Georgia and is harvested from crab traps by commercial crabbers as an incidental catch. *B. spiratus* is uncommon in the coastal waters of Georgia. In ten years of collecting mollusca, the author has collected only two live *B. spiratus:* one from 50 miles offshore of St. Catherine's Island and one from the main channel to Wassaw Sound, Georgia.

The sex ratios reported above agree well with those determined by Castagna and Kraeuter (personal communication) in Virginia but differ from those reported by Magalhaes (1948). Magalhaes (1948), as we did, found that females were larger than males, however, in North Carolina the sex ratio of male to female *Busycon carica* differed from 1:1, 1:2, or 3:1 depending on location and time of year. The high occurrence of females in the sample is probably due to whelks being protandric. Whelks mature as

TABLE 2.

Sex ratios of *Busycon carica*, *Busycon contrarium* and *Busycotypus canaliculatus* collected intertidally from Wassaw Sound, Georgia.

	B. carica		*B. canaliculatus*		*B. contrarium*	
	Males	Females	Males	Females	Males	Females
Number	16	179	3	21	0	57
Percentage	8	92	12.5	87.5	0	100
Average length ± S.D. (cm)	10.9 ± 2.8	14.8 ± 3.3	8.2 ± 1.1	13.5 ± 2.0	0	18.0 ± 2.1
Range (cm)	6.5 to 17.0	7.26 to 22.0	7.0 to 9.7	10.0 to 16.0	0	13.0 to 21.8
Ratio	1 to 11		1 to 7		0 to 57	

TABLE 3.

Species composition of *Busycon* and *Busycotypus* populations from different geographical areas of the United States and Mexico.

Source	Area	Dominant Species	2nd Abundant Species	3rd Species	Species Ratio
Summer et al.*					
1913	Woods Hole, Mass.	27 *B. canaliculatus*	5 *B. carica*		5:1
Wood and Wood*					
1928	Cape May, NJ	47 *B. carica*	6 *B. canaliculatus*		8:1
Coues					
1871	Fort Macon, NC	20 *B. carica*	2 *B. canaliculatus*	2 *B. contrarium*	10:1:1
Magalhaes*					
1948	Beaufort, NC	910 *B. carica*	61 *B. canaliculatus*	29 *B. contrarium*	33:2:1
Walker et al.					
1980	Savannah, GA	829 *B. carica*	214 *B. contrarium*	15 *B. canaliculatus*	55:14:1
Walker					
This Study	Wassaw Sound, GA	935 *B. carica*	244 *B. contrarium*	12 *B. canaliculatus*	78:20:1
Post*					
1899	Tampa, FL	45 *B. contrarium*	6 *B. spiratus*		7:1
Paine*					
1962	Alligator Harbor, FL	899 *B. contrarium*	211 *B. spiratus*		4:1
Hildebrand*					
1954	Corpus Christi, TX	123 *B. contrarium*	65 *B. spiratus*		2:1
Hildebrand*					
1954	Obregon, MX	16 *B. contrarium*	8 *B. spiratus*		2:1

* From Paine (1962)

males then lose their penis coverting to females at an older age. Smaller size male whelks are harder to find compared to larger size females.

Whelks are harvested by commercial fishermen in the coastal waters of Georgia by four methods: trawling with a modified shrimp net in the nearshore area, incidental harvesting while shrimping, harvesting them from crab traps, and collecting them by hand from intertidal to shallow water areas. Whelk trawling, usually from January to May, is the major commercial harvesting method (see Table 5) with most of the product being processed in Georgia and the meat sold as "conchs" to northern markets. Crabbers harvest *B. canaliculatus* as an incidental catch and their product is either sold to local whelk processors to be shipped north or are sold locally where it is primarily eaten by an ethnic group. Although crabbers harvest whelks year round, the major period of whelk collecting is during January to May periods. Crabbers only harvest *B. canaliculatus* since *B. carica* (Shaw 1960) and *B. contrarium* (personal observations) do not enter crab traps. Whelks collected commercially from intertidal areas are harvested by crabbers, clammers and oystermen and can be considered as an incidental catch to those fisheries. Commercial landings of whelks from intertidal gatherings are apparently not reported as such, but occur (personal observation), and may be included as landings by crab pot (Gordon Rogers, personal communication). Whelks are also harvested by hand from intertidal areas by sport fishermen (personal observations).

The most obvious result of this study is that the optimum times to commercially collect whelks form intertidal areas is during fall and spring. Peak densities of whelks occur during this time period and whelks are generally absent from the intertidal areas in summer and winter.

One area of research that needs investigating is the reproductive aspects of intertidal and subtidal whelk popula-

TABLE 4.

Population densities of *Busycon* and/or *Busycotypus* from different geographical areas.

Sources	Area	Given Density	Density Per Hectare
Carriker 1951	Little Egg Harbor, NJ	1/9 m^2	1077
Magalhaes 1948	Beaufort, NC	1/7 m^2	1363
Nichy and Menzel 1958	Alligator Harbor, FL	1/25 m^2	400
Kent 1983	Alligator Harbor, FL	4/2500 m^2	8
Walker			
This Study	Wassaw Sound, GA		243

TABLE 5.

Summary of whelk landings for the coastal waters of Georgia.

Year	Nearshore Whelk Season	Whelks Caught by 4 inch Mesh Net During Season (lbs.)	No. of Boats Licensed for Whelking	Whelks Caught While Shrimping (lbs.)	Whelks Caught by Crabbers in Whelk Season (lbs.)	Annual Crab Pot Landing of Whelks (lbs.)	Total Whelk Landings (lbs.)
1981	None	0	0	0	3,800		
1982	1 Jan. to 10 April	68,000	22	0	13,000	16,000	84,000
1983	21 Jan. to 1 May	149,000	34	3,400	13,000	37,000	189,400
1984	15 Feb. to 9 May	430,000	44	4,200	14,000	18,000	452,200
1985	1 Jan. to 3 May	174,000	35	46,000	19,000	20,000	240,000
1986	21 Feb. to 7 May	53,000	15	6,100	7,300**	12,000	71,000
1987	3 Feb. to 9 May	267,000	27*	0	4,900**	5,000	276,900

* Only 16 boats actually fished for whelks

** Poor crab landing years

All data from Gordon Rogers, Georgia Department of Natural Resources, Personal communication.

tions. Mating whelks during this study occurred in spring, although mating and egg laying also occurs in the fall. Whelk egg cases in coastal Georgia generally do not occur intertidally except on low spring water tides. Thus if whelks migrate into the intertidal areas in spring and fall to feed and mate and harvesting occurs in spring, will the females which are larger and easier to locate be removed from the populations before laying their eggs? Will the reproductive effort of whelks laying eggs in the fall be able to offset the loss of young during the spring harvesting? Presently, harvesting whelks from intertidal areas is fairly minor compared to nearshore harvesting, but with continued growth of the fishery and increases in demand for the product, these populations may experience heavy fishing pressures in the near future. Is there enough mating and egg laying occurring in subtidal populations in the creeks, rivers and sounds that the contribution in reproduction of intertidal whelks is insignificant or can subtidal populations from inshore areas repopulate whelk populations from the nearshore area? Trawling in the nearshore areas not only harvests whelks but also collects egg case strings, which are thrown overboard to wash up and dessicate on the beaches.

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ENUMERATION AND IDENTIFICATION OF HETEROTROPHIC BACTERIA ON OYSTER GROUNDS OF LONG ISLAND SOUND

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ABSTRACT A one-year study was conducted to identify the bacterial flora present in the water column above four oyster beds located in Long Island Sound, Connecticut. Monthly samplings indicated that Gram-negative rods, particularly the genera *Flavobacterium, Archromobacter, Pseudomonas,* and *Vibrio* predominated the flora isolated. Average bacterial counts were highest during early spring and lowest during late summer.

KEY WORDS: bacteria, *Flavobacterium, Archromobacter, Pseudomonas, Vibrio,* oyster beds

INTRODUCTION

Long Island Sound, an estuarine body of water bounded by New York and Connecticut shores, has long supported large populations of the economically important oyster, *Crassostrea virginica* (Gmelin) (Galtsoff 1964). Since World War I, the development of harbors associated with some of the richest oyster grounds in Long Island Sound has occurred concomitant with a sporadic, yet real, decline in the productivity of those beds. An earlier study by Murchelano and Brown, 1970 suggested that one of the reasons for a decrease in productive yield may be ascribed to bacteria pathogenic to *C. virginica*.

The present study was designed to characterize the bacteria isolated from the bottom water and surface water of three harbors and one river mouth that support populations of *C. virginica*. A later paper will address the pathogenicity of these bacterial isolates to *C. virginica*.

Three harbors New Haven, Bridgeport, and Norwalk, and one nearshore shellfish bed off Stratford, Connecticut, with populations of *Crassostrea virginica* were selected for this study (Figure 1). New Haven harbor has historically produced some of the best oyster sets in the United States. At the entrance of the Quinnipiac River into Long Island Sound, this harbor provides ideal estuarine conditions for the support of *C. virginica* populations. Since 1919, however, development of New Haven Harbor into an industrial port has forced the decline of the oyster industry in the area. While it still supports a rich oyster set in most years, the productive yield of marketable *C. virginica* has decreased dramatically (U.S. Dept. Interior 1970).

The Stratford shellfish beds, a non-industrial area fed by the industrially-polluted Housatonic River, has not been noted for its oyster production in recent years, yet it does support a small population of *C. virginica*. Historically, good oyster sets occurred there in the 1920's, but the oyster population declined to non-commercial levels in the 1950's and have remained non-commercial to this date.

Bridgeport Harbor is the site of a very heavily industrialized city port. The Harbor population of *Crassostrea virginica* may be characterized as sizeable and consistant in natural set, although it is heavily impacted by industrial pollution.

Outer Norwalk Harbor is a favorable site for the production of *C. virginica*. Marginally populated, it is not seriously impacted by residential or industrial pollution.

Thus, the three harbors and Stratford share the ability to support *Crassostrea virginica* yet have distinct charcteristics. Sampling from these four areas should permit the opportunity to determine whether such varied environments support similar or distinct microbial flora or whether the predominance of one bacterial genus over another shifts with changing environmental parameters.

MATERIALS AND METHODS

Monthly samples of surface and bottom water were collected at spring low tides from February 1980–January 1981 off New Haven (41°14′N latitude, 72°54.3′W longitude), Stratford (41°10′N, 73°6.9′W), Bridgeport (41°11.2′N 73°10.4′W) and Norwalk (41°2.5′N, 73°27.3′W), Connecticut. Loran C bearings and marked stakes were used to identify the oyster beds and allowed for repeated sampling from the same locations.

Water parameters of temperature, salinity, pH and dissolved oxygen were measured at each sampling station. Temperature and salinity were taken with a Yellow Springs Instrument Co. S-C-T meter (Model 33). Dissolved oxygen

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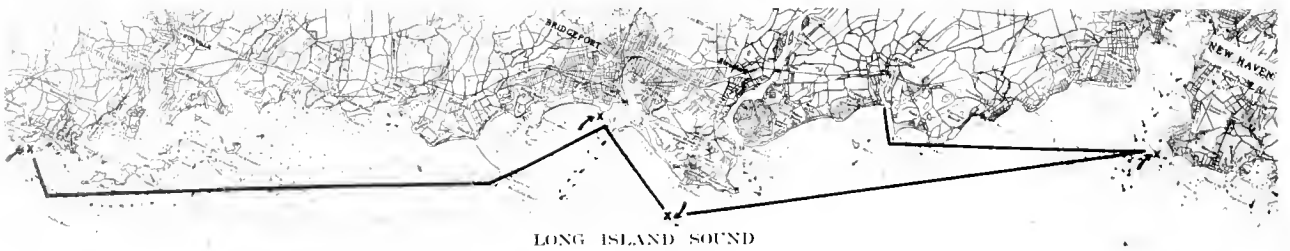

X = Natural Shellfish Bed, Sampling Site

Figure 1. Sampling stations within Long Island Sound, Connecticut.

measurements were made with a Yellow Springs Instrument Co. D. O. meter (Model 51). The pH was determined with an Orion digital pH meter (Model 211).

Surface water samples were collected in sterile bottles, whereas bottom water samples were obtained one meter above the sediment using sterile Sieburth sampling bulbs (Sieburth 1963).

All samples were plated within one hour of collection using the Buck and Cleverdon (1960) spread plate method. The isolation media used was Oppenheimer-ZoBell Reduced Medium (Oppenheimer and ZoBell 1952) and Thiosulfate Citrate Bile Salts Sucrose Agar (TCBS) (DIFCO). The dilution range was 10^{-1} to 10^{-6} and varied in accordance with the type of media used and the growth of colonies on the plates. The plates were incubated at 15°C for two weeks and were examined daily. At the end of two weeks, the plates were studied for total colony counts. All morphologically distinct colonies were then isolated for identification. Isolates were characterized according to the methods of Murchelano and Brown (1970) and identified to genus using the taxonomic scheme of Shewan et al. (1960).

RESULTS

Salinity levels for the sampling period ranged from 20.3 to 27.5 parts per thousand for surface water, and from 22.1 to 29.5 ppt for bottom water. pH values ranged from 7.4 to 8.4 for both surface and bottom waters. Dissolved oxygen levels for the one-year study ranged from 3.8 to 15.1 parts per million.

The majority of the morphologically dissimilar bacterial colonies recovered from Long Island Sound waters over oyster beds were asporogenous, Gram-negative rods. The genus *Flavobacterium* predominated, representing 41.9% of the bacterial colonies isolated for study, while *Achromobacter* represented 22.8%, *Pseudomonas* 17.4% and *Vibrio* 5.6%. Both *Flavobacterium* and *Vibrio* peaked during the summer; *Achromobacter*, on the other hand, was at its lowest level during this period and had its greatest abundance during the winter months. *Flavobacterium* had its lowest density during the winter, while *Vibrio* dropped to its lowest level during the fall. Unlike the others, *Pseudomonas* showed no significant seasonal variation.

The average bacterial count of the four oyster ground sites was highest during early spring. The count dropped steadily through the summer, except for a small increase in August, and reached a low during September. The average count peaked again in late fall. This seasonal variation in bacterial count did not correspond to variation in temperature (Figure 2). This may suggest that these bacterial counts are not directly tied to temperature alone but rather to other environmental factors (i.e., plankton blooms) in which temperature may be a limiting factor.

Mean bacterial densities ranged from a minimum of 5.3 $\times$ 10^3 colony forming units/ml (CFU/ml) in late summer to a maximum of 6.8 $\times$ 10^4 CFU/ml in early spring. The same pattern prevailed when bacterial counts from each oyster bed were examined separately (Figure 3, A-D).

Data collected from the New Haven site (Figure 3A) showed that its surface water tended to have a greater bacterial density than did its bottom water, with the exception of September. The other three sites showed a much closer correlation in bacterial density between surface and bottom waters.

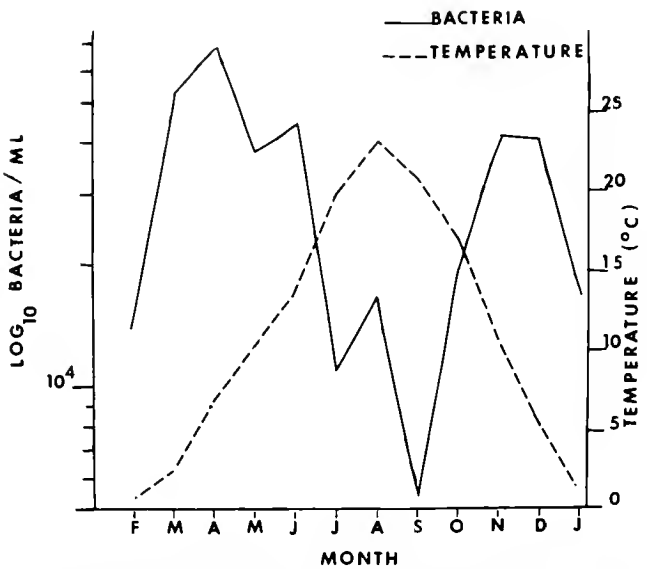

Figure 2. Variation in average total bacterial count and temperature in Long Island Sound.

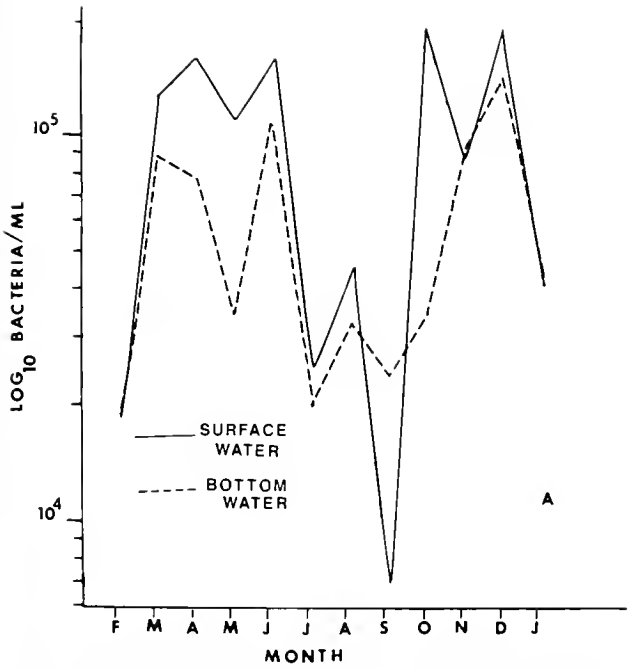

Figure 3A. Total bacterial plate counts of surface and bottom water for the New Haven site.

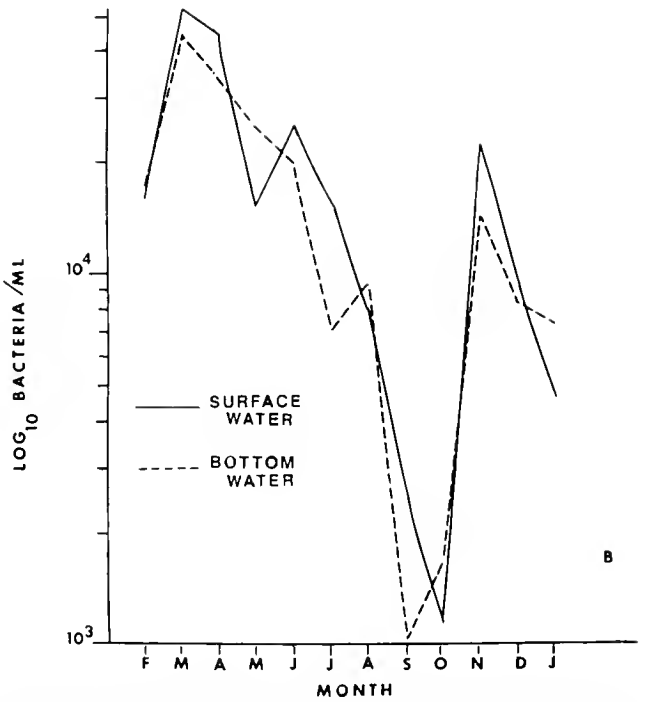

Figure 3B. Total bacterial plate counts of surface and bottom water for the Stratford site.

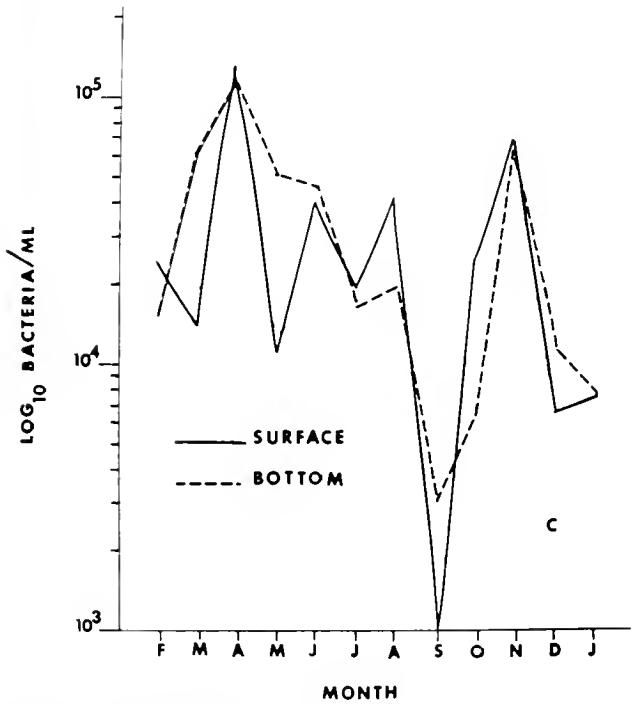

Figure 3C. Total bacterial plate counts of surface and bottom water for the Bridgeport site.

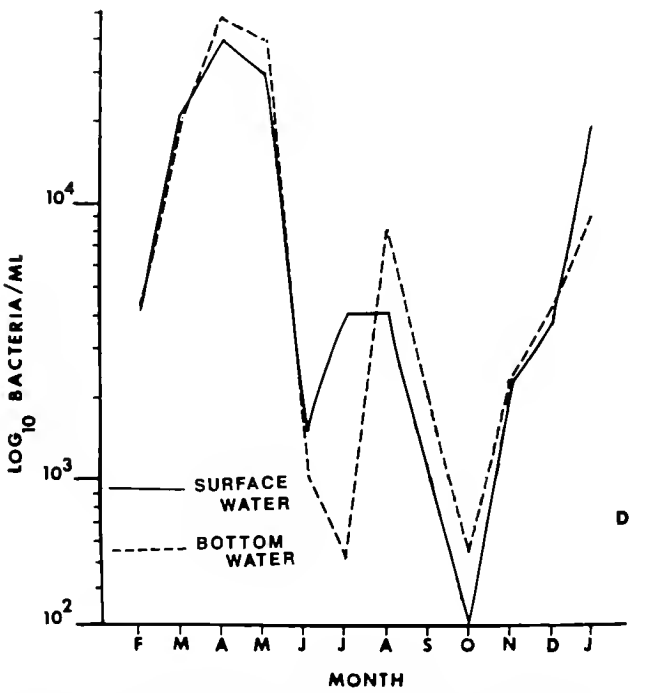

Figure 3D. Total bacterial plate counts for the surface and bottom water for the Norwalk site.

DISCUSSION

The present study indicates that the four study sites support similar microbial flora, with the genera *Flavobacterium, Achromobacter, Pseudomonas,* and *Vibrio* being the predominant isolates from each site. However, the density of the genera differs at each site, likely due to several factors working to limit a suitable nutrient supply for the microorganism.

The seasonal fluctuation in total bacterial density over

oyster beds corresponds to the seasonal cycle of phytoplankton noted by Riley and Conover (1967). Both bacteria and phytoplankton reach major peaks in spring and late fall.

The four bacteria genera examined in this study varied in seasonal distribution. That both *Flavorbacterium* and *Vibrio* peaked during the summer may be due to an association with zooplankton. Kaneko and Colwell (1973) observed that *Vibrio parahaemolytics* was released from the sediments of the Chesapeake Bay during the late spring and associated with zooplankton, both *Vibrio* and plankton increasing in density as the water temperature rose. Most pseudomonads are free-living organisms (Volk 1982), which may help to explain why this genus exhibited no significant seasonal variation. *Achromobacter* was most abundant during the winter months. This is likely related to the life cycle and development of this microorganism.

The surface water in New Haven had a greater bacterial density than its bottom waters for most of the year, unlike the other sites which did not show appreciable differences between surface and bottom water counts. This observation may be explained by the rich supply of nutrients that exists in the surface layers of New Haven Harbor or by harbor dredging which was observed during the sampling periods. The decrease in bacterial density observed in September may be due to a concurrent seasonal plankton decline.

Perhaps the most significant observation to be made from this study is that the four predominant genera of bacteria isolated from waters over the oyster beds studied have species or varieties known to be pathogenic to the oyster, *Crassostrea virginica* in hatchery or laboratory settings (Tettelbach et al. 1984, Tubiash 1975, Elston et al. 1981).

Further studies will establish whether the isolates obtained from nature in this study exhibit any pathogenic action toward *C. virginica*.

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The authors appreciate the reviews of Drs. Anthony Calabrese and Sandra Shumway. We thank Dr. Steven Tettelbach for data collection.

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ENDOCYTOSIS AND LYSIS OF BACTERIA IN GILL EPITHELIUM OF *BATHYMODIOLUS THERMOPHILUS, THYASIRA FLEXUOSA* AND *LUCINELLA DIVARICATA* (BIVALVE, MOLLUSCS).

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ABSTRACT The gills of the hydrothermal vent mussel *Bathymodiolus thermophilus* and two Lucinacea from reduced littoral biotopes, *Lucinella divaricata* and *Thyasira flexuosa*, contain large numbers of bacteria within epithelial cells, the bacteriocytes. Ultrastructural studies reveal the presence of bacteria tightly associated with the bacteriocytes microvilli and also plasma membrane invaginations which progressively isolate bacteria within endocytotic vacuoles. This suggests that in these species direct "infection" of the bivalves from an environmental stock of bacteria may occur. The envacuolated bacteria appear to undergo progressive lysis and numerous myeline-like figures resembling residual lysosomal bodies then appear in the cell host cytoplasm.

KEY WORDS: *Bathymodiolus, Thyasira, Lucinella*, hydrothermal vent, bacteria

INTRODUCTION

Symbioses between intracellular chemoautotropic bacteria and invertebrates were first described in animals from hydrothermal vents (Cavanaugh et al. 1981, Felbeck 1981). Since the original discovery, this type of symbiosis has been discovered in numerous marine invertebrates inhabiting biotopes where oxygen and reduced sulfur compounds are simultaneously available. This heterospecific association takes place in the trophosome tissue of pogonophorans (Cavanaugh et al. 1981, Felbeck 1981, Southward 1982), the subcuticular space of gutless marine oligochaetes *Phallodrilus* (Felbeck et al. 1983a) and the gills of many bivalve molluscs including the Vesicomyidae *Calypogena magnifica* (Cavanaugh 1983, Fiala-Médioni 1984), *Calyptogena pacifica* (Cavanaugh 1983), *Calyptogena laubieri, Calyptogena phaseoliformis* (Fiala-Médioni and Le Pennec 1988), Mytilidae, *Bathymodiolus thermophilus* (Cavanaugh 1983, Felbeck 1983, Le Pennec and Hily 1984), the genus *Solemya* (Cavanaugh 1983, Felbeck et al. 1983b) some species of Thyasiridae (Dando and Southward 1986, Reid and Brand 1986, Southward 1986) and Lucinidae (Fisher and Hand 1984, Dando et al. 1985, 1986, Schweimanns and Felbeck 1985, Reid and Brand 1986, Le Pennec et al. 1987).

In all these species symbionts have been localised ultrastructurally and shown biochemically to be chemoautotrophic. The oxidation of reduced sulfur compounds from the external environment causes the conversion of dissolved carbon-dioxide into organic compounds by these bacteria. Then these organic compounds become available to the heterotrophic host as demonstrated by the carbon isotope composition ($\delta^{13}C‰$) of various tissues (Spiro et al. 1986) and histoautoradiographic studies (Fisher and Childress 1986). Recently Southward (1987) has reviewed the role of symbiotic chemoautotroph bacteria in the nutrition of benthic invertebrates.

All observations on the gills of bivalves containing chemoautotrophic bacteria reveal bacterial lysis inside the bacteriocytes. This is particularly evident in some species such as *T. flexuosa* (Southward 1986) and *L. divaricata* (Le Pennec et al. 1987). One of the main areas not yet elucidated is how the bacteria colonize the gill epiderm.

The question of whether symbionts are transmitted through the sexual cycle of the host or are acquired from other sources has not been fully investigated to date. Endosymbiont transmission in invertebrate–microorganism symbiosis may proceed by one of three ways: vertical transmission which may include incorporation of symbionts in or on the gametes of the host parent; horizontal transmission which involves contamination of symbionts between contemporary hosts; or reinfection of the new host generation from the environmental stock of bacteria. Giere and Langheld (1987) report that vertical transmission of chemoautotrophic symbionts for the extracellular marine oligochaetes symbiosis *Phallodrilus leukodermatus* and *P. planus* occurs when eggs are infected at oviposition from bacteria extruded from the adult genital pad. Gustafson and Reid (1988) argue that perpetuation of the symbiosis in the gutless bivalve *Solemya reidi* proceeds by vertical transmission, although bacteria were not seen in or on gametes nor in gills of juveniles. These authors hypothesize that bacteria develop from a cryptic "packaging form" within granular vesicles present in the larval test.

The present study was designed to investigate of bacterial endocytosis and bacterial lysis in some species of sym-

biont-containing bivalves living in the hydrothermal ecosystem and in reduced littoral biotopes.

MATERIALS AND METHODS

Samples of *Bathymodiolus thermophilus* were collected at 2620 m-depth during the Biocyatherm and Biocyarise cruises organized by IFREMER (Institut Français de Recherche pour l'Exploitation de la Mer) in March 1982 and March 1984 on the active hydrothermal sites of the east Pacific Rise, of the Mexican coasts (12°59′N and 103°56′W).

Specimens of *Lucinella divaricata* were collected from an intertidal seagrass bed at Morgat, Crozon (France). Specimens of *Thyasira flexuosa* were dredged from Brest harbour by the IFREMER oceanographic vessel "Sainte Anne du Portzic".

After dissection, portions of the gills were fixed in 3% glutaraldehyde in a 0.4 M cacodylate buffer at pH 7.8, post-fixed in 1% osmium tetroxide, embedded in Spurr resin, ultra-sectioned and stained with 7% uranyl acetate and 0.1% lead citrate before examination using a Jeol 100 CX microscope. For each species, several specimens were examined.

RESULTS

Bacterial Endocytosis

According to Herry et al. (1988) each gill filament of the species here studied can be divided into three parts: two ciliated zones, separated by a lateral zone. Only the bacteriocytes of the lateral zone which occupy the main part of the filament are considered. These bacteriocytes are large spherical cells with diameter ranging form 20 to 40 μm. Their nuclei are in a basal position and some glycogenic particles, some mitochondria and some electron dense globules of different sizes are observed in their cytoplasm. The main part of the cellular volume is occupied by vacuoles containing bacteria (Figure 1a and c). The basal lamina is more or less convoluted. The apical bacteriocyte surface is covered with numerous microvilli associated with a thick glycocalyx (Figure 1a, b and d). Bacteria from the extracellular space seem to be "caught" by bacteriocyte microvilli (Figure 1a). Numerous plasmic membrane invaginations which progressively isolate microorganisms into endocytosis vacuoles are observed (Figure 1b). In all species, the bacteria are found in vacuoles in the apical portion of the bacteriocyte near the cell surface. *L. divaricata* bacteriocytes house only one symbiont visible per host-cell vacuole in most of the sections (Figure 1e), while numerous bacteria per host-cell vacuole are visible in cross sections of *T. flexuosa* and *B. thermophilus* bacteriocytes (Figure 1a and c).

Symbiotic Bacteria

The bacteria observed in endocytotic vacuoles are of different sizes and shapes. They are coccoïd or short rods and measure 0.3–0.75 μm × 1–2.5 μm. They have a double membrane which is characteristic of Gram negative type (Figure 1e). The cytoplasm, usually clear, is sometimes filled with glycogen particles, as seen in thin sections of *L. divaricata* (Figure 1e). Clear vesicles occur in the gill endocellular bacteria of *L. divaricata* (Figure 1e); similar vesicles, identified as sulfur granules, were reported in sulfur oxidizing bacteria of other bivalve species (Dando et al. 1985, Fisher and Hand 1985).

The nucleoïd, when visible, has a filamentous structure (Figure 1d). A specimen of *T. flexuosa* collected in polluted mud from Brest harbour shows numerous bacteriophages in the gill endocellular bacteria (Figure 1d).

Bacteria Lysis

In all species of bivalve containing bacteria studied to date, a marked bacterial lysis at the basal part of the bacteriocytes is observed. The most characteristic bacterial lysis is observed in the Lucinidae bacteriocytes. Cytoplasmic glycogenic particles of the bacteria first disappear and intracytoplasmic vacuoles are formed (Figure 2a and b). These vacuoles, whose boundaries are emphasized by perivesicular electron dense granules, increase in size and fuse together in a large vacuole. Finally all the bacterial contents disappear and electron dense granules are seen at the basal part of the bacteriocyte (Figure 2c). In some bacteriocytes all the bacteria are lysed and the greatest portion of the cell volume is occupied by phagosomes and lipidic globules (Figure 2d). Lipidic globules are always associated with bacterial lysis (Figure 2c and d). In *T. flexuosa* harboring

Figure 1. Endocytosis and lysis of chemoautotrophic bacteria in gill epithelium of *Bathymodiolus thermophilus*, *Thyasira flexuosa* and *Lucinella divaricata*.

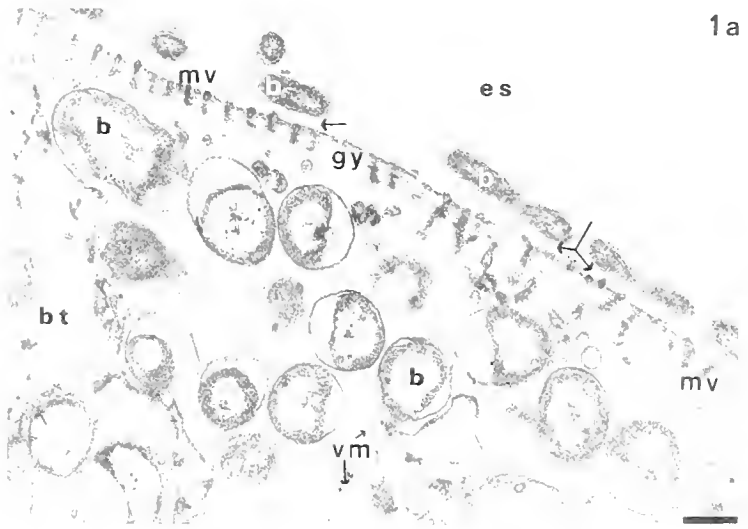
a) Bacteria (b) in the extracellular space (es) tighly associated to the microvilli (arrows) in *T. flexuosa*. mv: microvilli, gy: glycocalyx, vm: vacuolar membrane. Scale bar = 0.20 μm.

b) Endocytosis of bacteria (b) in *T. flexuosa* bacteriocyte (bt) Scale bar = 0.20 μm.

c) Bacteria (b) envacuolated in *B. thermophilus*. Scale bar = 0.20 μm.

d) Bacteriophages (bt) in bacteria of *T. flexuosa*. n: nucleoid, mv: microvilli, vm: vacuolar membrane, cy: cytoplasm. Scale bar = 0.10 μm.

e) Beginning of bacterial lysis in *L. divaricata*. formation of vesicles (v) in the cytoplasm, mainly at the peripherie, appearance of glycogen particles and perivesicular dense granules (arrows). Scale bar = 0.25 μm.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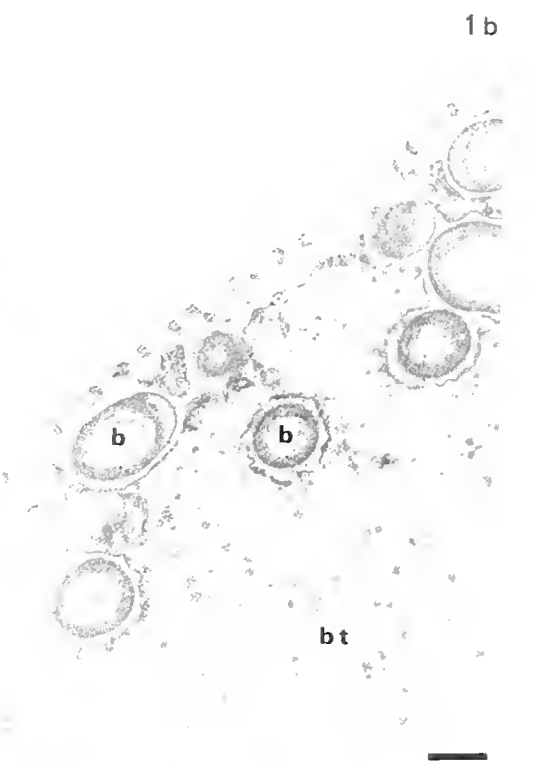
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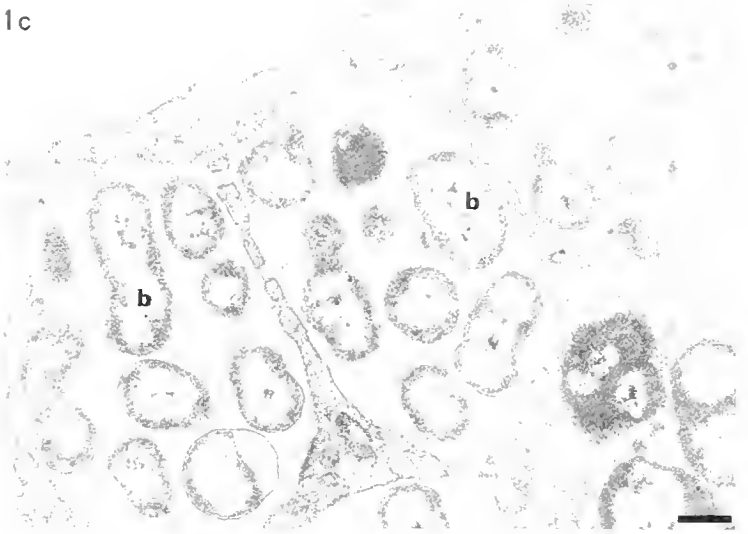
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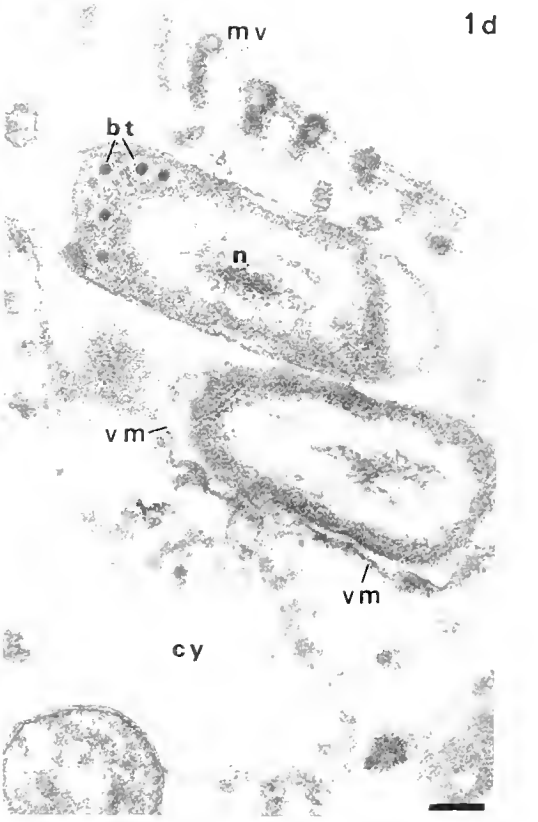
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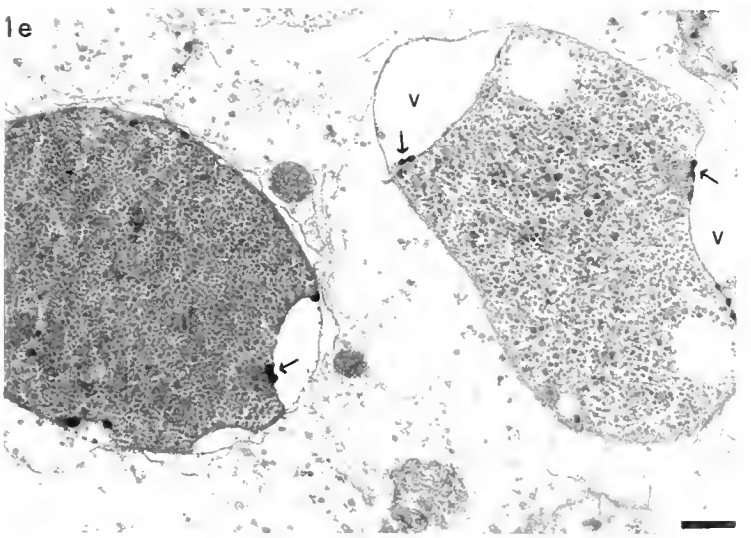
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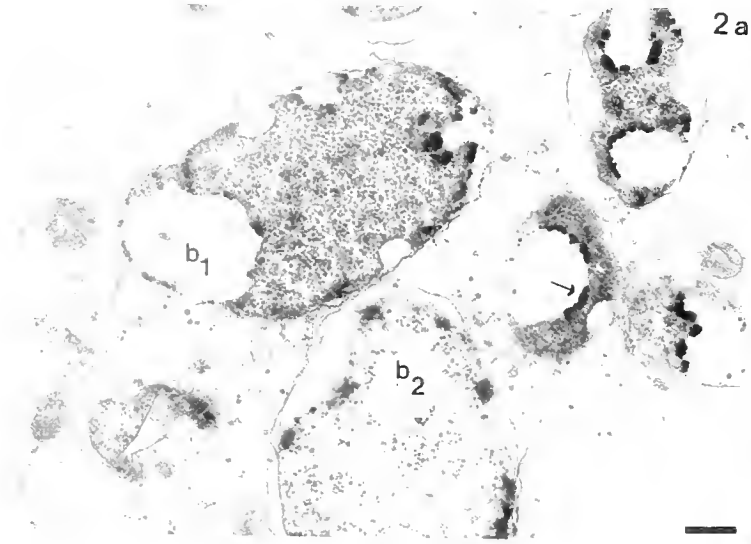
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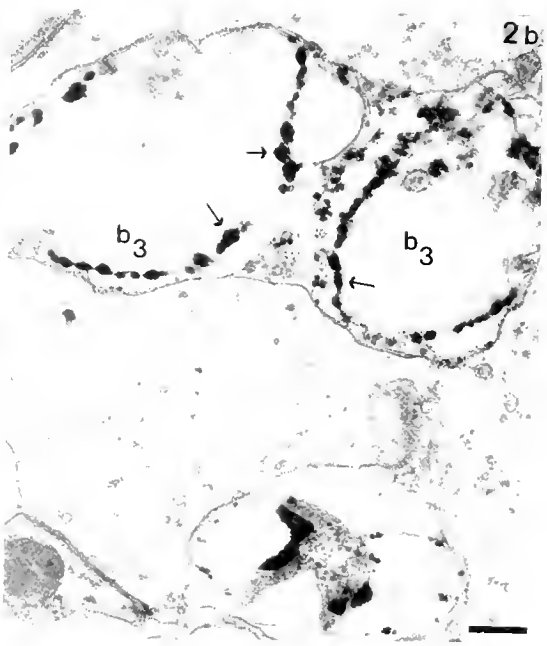
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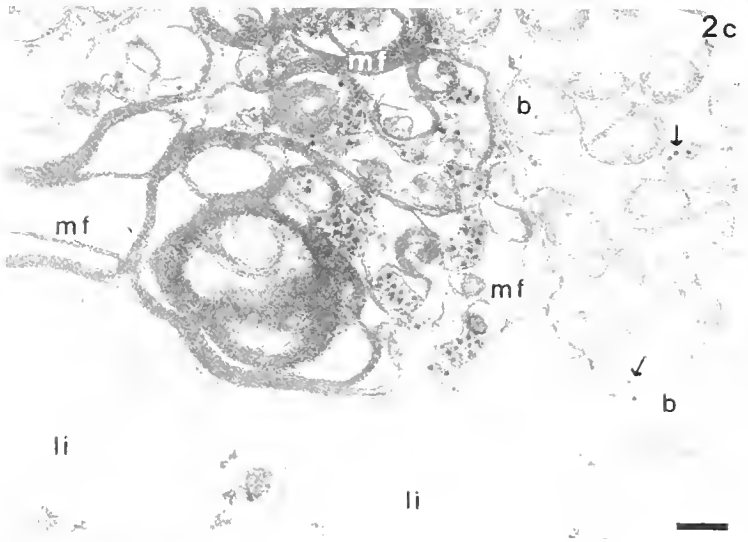
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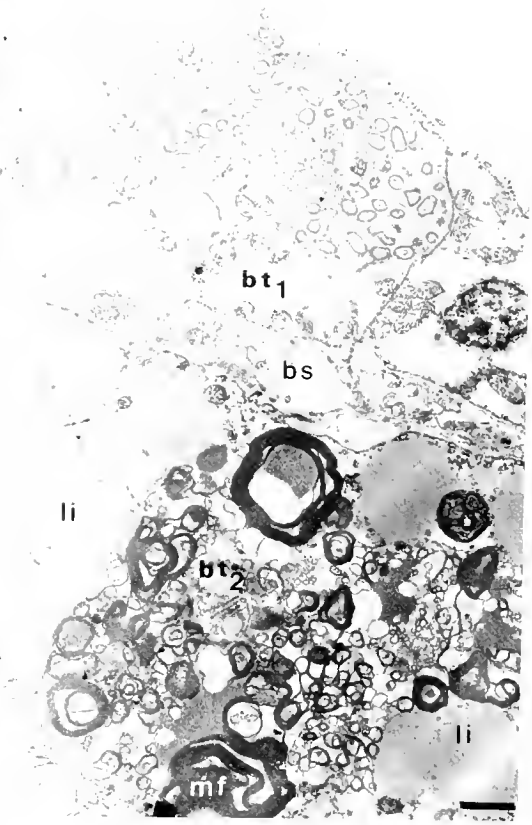
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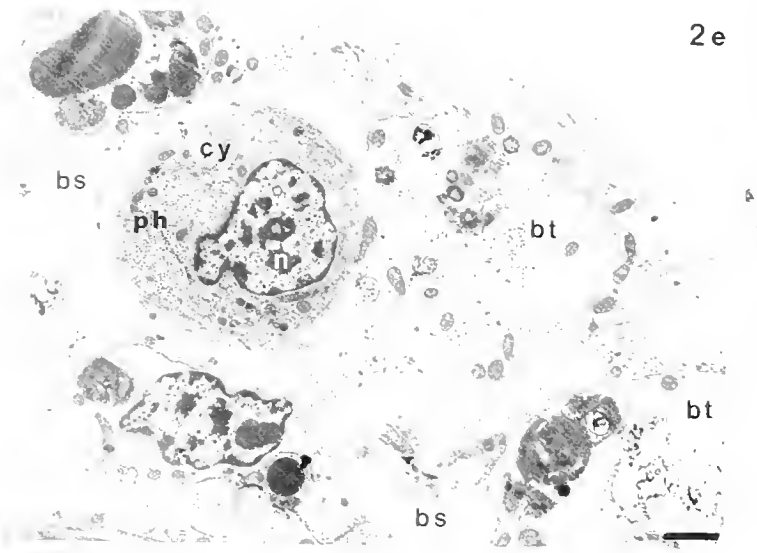
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bacteriophages in their endocellular bacteria, many virus-like particles are seen included in myelin-like figures coming from bacterial lysis (Figure 2c).

Hemocytes are frequently observed, closely associated with bacteriocytes whose basal lamina is highly convoluted (Figure 2e). These hemocytes, which contain granules of varying density, show numerous pseudopodial-like expansions of the cytoplasm in close contact with the basal membrane of bacteriocytes. Furthermore, the same kind of phagocytic hemocytes can be observed in the gill epithelium (Figure 2e).

DISCUSSION

As the work on invertebrates inhabiting sulfide rich habitats progresses, new species harboring endocellular chemoautotrophic bacteria in their gill epithelium are discovered. The large number of bacteria in these animals does not seem to harm the host tissues. On the contrary, the gills containing symbionts are more voluminous than usual. For example, gill weight of *Lucinoma aequizonata* averaged 35 ± 2% of tissues total weight excluding valves compared to 10 ± 2% in *Mytilus edulis* (Distel and Felbeck 1987). In spite of a reduced capability to feed normally by means of the digestive tract, many of these animals grow large. This is particularly noticeable on the hydrothermal vents where the mussel *Bathymodiolus thermophilus* can reach 18 cm (Kenk and Wilson 1985) and the clam *Calyptogena magnifica* 26 cm (Boss and Turner 1980). The biomass developed by these hydrothermal mollusc bivalves which reach 10.1 kg/m^2 (Hessler and Smithey 1983) is much greater than in those usually found at this depth which range from 0.1 to 10 g/m^2 (Somero et al. 1983). In the littoral reduced biotope, the Lucinacea are often the most important fauna and even if the sizes of the different species are small, their density can be high. Thus Monnat (1970), reported that *Lucinoma borealis* attains 1500 m^{-2} in some seagrass beds from the west coast of Brittany (France) while the density of non symbiont-containing bivalves is between 1 and 10 animals · m^{-2}. In these conditions we can think that the high biomass value of these invertebrates depends on the intensity of the trophic role played by the gill with the help of symbiotic bacteria.

The presence of chemoautotrophic sulphide oxidizing bacteria in a large number of the bivalve gills studied here has been demonstrated by a combination of biochemical and electron-microscopic studies (Dando and Southward 1986, Fiala-Médioni et al. 1986, Le Pennec et al. 1987). In all these species, each bacteriocyte, separated from the sea water by a single extremely thin layer of ciliated epithelial cells, has equal exposure to the external environment. Furthermore, the densely packed microvilli of the bacteriocytes apical pole increases the available surface area of this tissue for gas and solute exchange and probably for bacteria endocytosis. This suggests that bacteriocytes have a strong demand for gas and/or exchange with the external environment. A careful balance from oxygen and sulfide concentration are essential to the survival of sulfide oxidizing bacteria, high sulfide can be toxic but undergoes spontaneous oxidation (Küenen and Beudeker 1982). Dando et al. (1985) and Reid and Brand (1986) proposed a mechanism where oxygen and sulfide levels within the mantle cavity are controlled by balancing current flow between the anterior inhalant opening receiving ambient sea water and the posterior inhalant opening receiving interstitial water from the anoxic sediments.

The water flow entering the gill cavity transports microorganism from sediment water surrounding the host to the bacteriocytes. According to Southward (1986), the symbionts live strategically close to the water flow between the gill filaments at the point where it has just been cleared of most particles by the eulaterofrontal cilia. Among these microorganisms might be some sulfur oxidizing bacteria which could attach to the microvilli of the bacteriocyte and later undergo endocytosis.

There are no data in the literature concerning "recognition" of the microorganisms by the gill cells. We can suppose that the first step is the linkage between the glycocalyx polysaccharidic fibres and the bacteria membrane polysaccharides, or a bacterium becoming entangled by the glycocalyx fibres which could bring the symbionts nearer the host cell cytoplasmic membrane. If there is a linkage it could be of polar type or on the contrary by means of a lectin. In the last case, the interaction would be specific and bacteria having other polysaccharides would not adhere to the host cells. Endocellular symbiosis must involve symbionts that are immune from the defense mechanisms of the hosts and whose metabolic capabilities have been adjusted to those of the bivalve. Further cytochemical investigations are necessary before an answer can be found.

In some bivalves containing chemoautotrophic bacteria it appears that direct infection of the hosts from an environ-

Figure 2. Lysis of intracellular gill bacteria in *Thyasira flexuosa* and *Lucinella divaricata*.

a) and b) Resorption of bacteria content until its complete disparition (b_1, b_2, b_3) in *L. divaricata*. The cytoplasm limits are underligned by electron-dense granules (arrows). Scale bar = 0.20 μm.

c) Intact endocellular bacteria (b), some of them show bacteriophages (arrows) and lysed bacteria aggregated among myelin-like figures (mf) in *T. flexuosa*. li: lipid granules. Scale bar = 0.25 μm.

d) Portion of gill epithelium of *T. flexuosa* showing bacteriocytes containing intact bacteria (bt_1) and remains of bacteria lysis (bt_2). bs: blood space, li: lipid granules, mf: myelin-like figures. Scale bar = 0.10 μm.

e) Phagocytic hemocyte (ph) of *L. divaricata* in the way to be expelled. n: nuclear, cy: cytoplasm, bt: bacteriocyte; bs: blood space. Scale bar = 0.70 μm.

mental stock of bacteria may occur. De Burgh and Singla (1984) noticed bacterial colonization and endocytosis on the gill of a new gasteropod species from a hydrothermal vent. It is hypothesized that endosymbiont transmission may proceed in other ways. In the gutless bivalve *Solemya reidi*, Gustafson and Reid (1988) believe that vertical transmission occurs from parent to offspring with recognizable bacteria developing in the larval test tissues from which they are released in the mantle cavity. In *B. thermophilus* male and female gametes were recently studied in detail (Herry and Le Pennec 1987) however no evidence of the presence of bacteria or bacterial rudiments in the sexual cells was observed. This reinforces the hypothesis of gill epithelium bacterial colonization from the environment. In these species, we can consider that it is only after larval metamorphosis that the capability for bacterial endocytosis occurs, during development of the gill filaments.

When bacteria are envacuolated their cellular volume increases and there is an accumulation of metabolites in their cytoplasm. The microorganisms are progressively degraded until total lysis. In the bacteriocytes, numerous pigment granules are observed in the symbionts themselves. Electron micrographs show that these structures contain an abundance of membrane whorls or myelin-like figures which are found in residual lysosomal bodies. Some of the bacteriocytes appear almost filled with huge phagosomes containing the remains of the lysis and numerous lipidic globules. We suppose that these cells desquamate and are replaced by the intercalary cells which are observed to be scattered among the bacteriocytes in all the symbiotic bivalves (Herry et al. 1988).

The bacteriophages observed in the bacteria of *T. flexuosa* could be used as a marker of the stage of development of the microorganisms. The lysis achieved, the bacteriophages are abundantly found in the phagosomes. This is confirmed by the integration in these structures of products not degraded by the lytic enzymes. Evidence that symbiotic bacteria are digested in host bacteriocyte in phagocytic vacuoles has been observed in thyasirid bivalves (Southward, 1986), gutless oligochaetes (Giere and Langhed 1987) and, to a lesser extent, in *Riftia* (Bosch and Grassé 1984). This may serve as a source of fixed carbon for the host and/or as a method to prevent excessive proliferation of bacteria in invertebrates.

Up to now there have been no data concerning the role played by the hemocytes in the heterospecific bacteria-bivalve relation. Gill observations of different species show that the hemolymphatic system is well developed and suggest that hemocytes, which possess a high capacity for phagocytosis and storage and a great mobility, could play an important part in gill detoxication. The indentations of the basal membrane of bacteriocytes suggest that intense exchanges could occur between the symbiont-containing cells and the blood space. Furthermore, some hemocytes with cytoplasm almost filled with electron-dense granules have been seen being extruded from the gill epithelium.

Our results suggest that in some species inhabiting particular biotopes such as hydrothermal vents and reduced littoral sites, the heterospecific bacteria-bivalve relationship may be set up by the environment. Electron micrographs reveal bacteria undergoing endocytosis, which are progressively lysed in the host bacteriocytes. We think that bacterial biochemical activity and bacterial lysis provide metabolic carbon to the host bivalves, but further research is required to make any definitive statements relative to that hypothesis.

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PROCEEDINGS OF THE LOUISIANA OYSTER INDUSTRY SYMPOSIUM

Presented at the 80th Annual Meeting

NATIONAL SHELLFISHERIES ASSOCIATION

New Orleans, Louisiana

June 26–30, 1988

Convened and edited by

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INTRODUCTION TO THE LOUISIANA OYSTER INDUSTRY SYMPOSIUM

Louisiana is now the nation's leader in oyster production. For those of us concerned with the Louisiana oyster industry this is no cause for celebration, since our premier status is mostly the result of the decline of the Chesapeake Bay industry, while Louisiana has maintained historical levels of production. In good years today, we produce as many or more oysters as were produced in good years during the early part of this century. The effort expended on oyster cultivation, however, is now greater and per capita harvests have declined.

The central problem of the Louisiana oyster industry is

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The central problem of the Louisiana oyster industry is that productive oyster grounds are being rapidly diminished. The intrusion of salt water from the Gulf (due to river channelization and canal building) brings predators and parasites that push the productive zone landward. Encroaching sewage pollution (from up-estuary) pushes the approved zone seaward. The oyster industry thus has the potential of being "squeezed out."

Despite problems associated with environmental degredation and manipulation, the Louisiana oyster industry is maintaining itself. It does so by expending more effort on cultivation and fishing, a leasing policy which provides adequate incentives to oystermen, and a state program which produces seed oysters for bedding on private leases.

The warm brackish waters of coastal Louisiana have provided a bountiful harvest of oysters and other seafood. Nature provided adequate spatfall, and the extensive, even remote, estuaries almost seemed immune from wholesale pollution. Yet, urbanization and industrialization have taken their toll. To deal with these problems there will likely be an infusion of new technologies into the Louisiana oyster industry. Some of these developments, though perhaps testimonies to our technological cleverness, are indications of our ecological failures. Whereas nature once provided adequate spatfall, man operates oyster hatcheries; where pristine waters flowed, man builds depuration plants.

Problems facing the industry are being addressed. New and expanded efforts to control sewage pollution are being made, plans are being formulated to divert fresh water from the Mississippi River into oyster-producing areas, and public attention has been focused on the need for more processing and increased "value-added" on Louisiana seafood products.

On June 30th 1988, a special symposium on the Louisiana oyster industry was held in New Orleans in conjunction with the 80th Annual Meeting of the National Shellfisheries Association. Topics of current and broad interest (i.e., to both oystermen and shellfish biologists) were presented by representatives from industry, government and academia. The purpose of the symposium was to reflect upon the industry's past, assess its present status, look toward the future, and make these management techniques, socio-economic issues, and research accomplishments available to all.

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ADMINISTERING THE LOUISIANA OYSTER FISHERY

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ABSTRACT Louisiana's oyster production has varied little dating back to the early 1800's. However, during the last 5 years it has increased slightly, now averaging approximately of 12.5 million pounds. The management of these fisheries has been entrusted to the Louisiana Department of Wildlife and Fisheries. The productive areas in coastal Louisiana are divided between those which can be leased by Louisiana residents for private oyster farming, and those areas designated as "Public Oyster Seed Grounds" available for both seed oyster production and direct commercial harvest. The administration of the privately leased areas consists of fielding survey crews to physically place and keep track of more than 311,000 acres presently under lease from the state. The administration and management of the "Public Oyster Seed Grounds" requires the sampling of these grounds to determine the available supply.

KEY WORDS: management, oysters, Louisiana

INTRODUCTION

Oyster (*Crassostrea virginica*, Gmelin) production in Louisiana during the last five years has averaged over 12.5 million pounds annually. This production has recently been valued at approximately 30 million dollars dockside and some economist have projected that this value is as high as 90 million dollars the retail level. Louisiana production has ranked the state first among Gulf states and for the last three or four years, first nationwide. This national ranking has been mostly due to the decline of the east coast oyster fisheries. The Louisiana oyster industry is labor intensive and, as such, is a large employer within the coastal community. Annually, in excess of some 2,000 harvesters are licensed along with ~200 oyster shop or retail establishments. In addition to its considerable economic impact, this industry is of great importance to the culture and heritage of coastal communities in Louisiana.

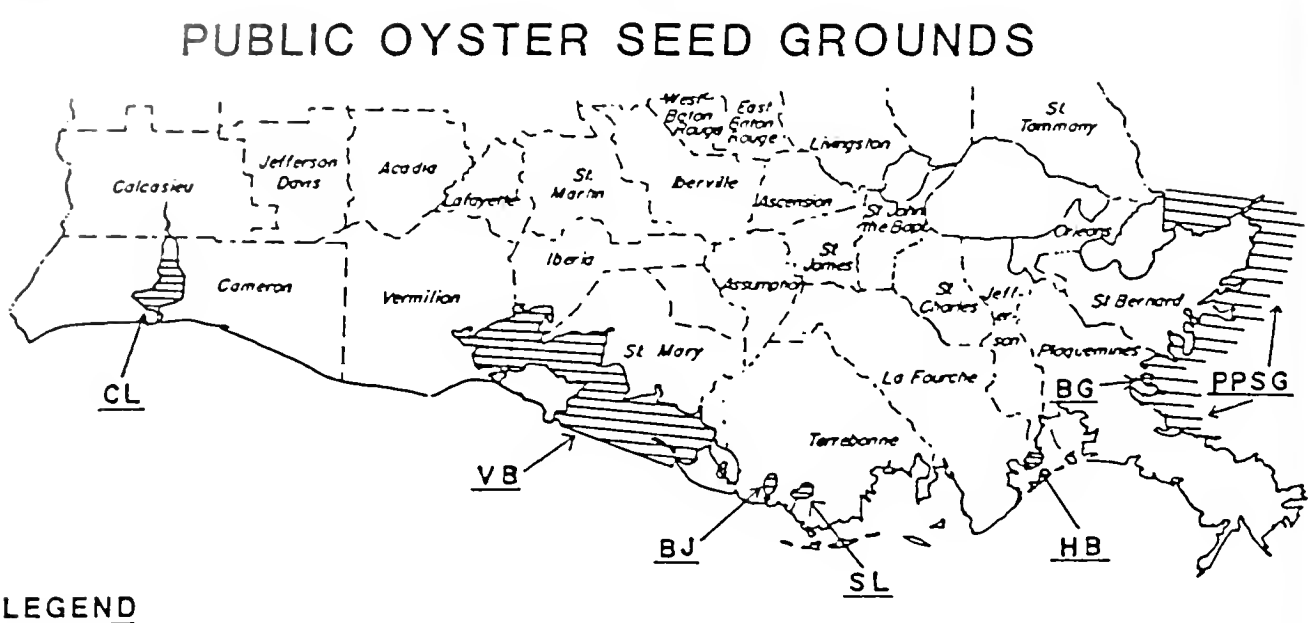
The large oyster production attributed to this state, as well as its consistency, is a direct result of the 8 million acres of estuarine environment along Louisiana's coast. The area is vast and variable enough to always have some coastal areas involved in oyster production. Aside from the vastness of estuarine areas, the consistency of harvest can be attributed to a combination of successful management practices and a willingness on the part of the industry to evolve. Oyster producing waterbottoms in Louisiana include both state-managed public grounds (ca. 2,000,000 acres) and privately-managed leased grounds (ca. 3,000 acres) (Figure 1).

The public grounds include most of the state's traditional, naturally-productive reef areas. Management of the public grounds, which is the responsibility of the Department of Wildlife and Fisheries, has been historically directed toward providing seed oysters for bedding on private grounds. An exception to this is the Calcasieu Lake tonging areas from which only marketable oysters may be taken. Management measures for the public grounds include harvesting restrictions, such as seasons and size limits, and enhancement projects such as cultch planting and freshwater diversions.

Essentially all remaining oyster growing areas in the state are available for private leasing. This includes existing as well as potential growing areas. Much of the privately leased area is not naturally productive but rather is used for bedding seed oysters. An individual may acquire as many leases as he desires provided the total area leased does not exceed 1000 acres. Leases are granted for a period of 15 years with the lessee given the first right of renewal. The annual rental for oyster leases is currently two dollars per acre. The oyster industry in Louisiana is based to a large degree on the cultivation of oysters on privately controlled waterbottoms rather than on the harvest of oysters from public waterbottoms. The Department controls the state waterbottoms with respect to the marine fishery resources. It leases suitable waterbottoms to private individuals who then culture oysters on these leases and make the oysters available for sale to the public. The activities and objectives of the oyster subprogram are, to a large extent dictated by the nature of the industry in Louisiana.

The following will be a summary of the Administrative efforts to maintain this production:

1. *Oyster Leasing*. There are over 2,000 people who hold more than 9,000 individual leases and more than 311,000 acres of state waterbottoms. These leases are issued for 15 year periods. This subprogram performs the survey work (Figure 2) required to establish these leases and issues lease plats to the lessee, giving them legal claim to the water bottom leased from the state. In addition to surveying and resurveying leases, an ongoing project is nearly completed that will establish geographic markers in the marshes of Louisiana adjacent to the oyster producing waterbottoms. As a result, future survey work will be more accurate and be accomplished in a shorter time span. Up-to-date maps of the coast



LEGEND

PPSG—PRIMARY OYSTER SEED GROUNDS
BG—BAY GARDENE OYSTER SEED RESERVATION
HB—HACKBERRY BAY OYSTER SEED RESERVATION
SL—SISTER LAKE OYSTER SEED RESERVATION
BJ—BAY JUNOP OYSTER SEED RESERVATION
VB—VERMILION BAY OYSTER SEED GROUNDS
CL—CALCASIEU LAKE PUBLIC TONGING GROUNDS

Figure 1. Louisiana Public Oyster Seed Grounds, Oyster Seed Reservation and Public Tonging Grounds.

which indicate the location of all leases and lease applications are maintained for the use of the subprogram, lessees and other interested parties. Since survey fees, lease rentals and other charges are required, a significant amount of accounting effort is needed.

2. *Seed Grounds/Public Grounds*. Since the typical oyster fisherman leases a specific site from the state,

Figure 2. Oyster lease surveying in coastal Louisiana.

he loses the mobility enjoyed by other fishermen (i.e. shrimpers or finfishermen). These other fishermen are able to follow the commercial fish stocks and harvest them in different locations. The oyster lessee, however is restricted to his own lease (except during open seasons on "Public" reefs). Environmental conditions fluctuate in coastal Louisiana to the point that young "seed" oysters may not settle on many leases. In order to provide the oyster lessee with a source of young oysters and thereby reduce the fluctuation of oysters available to the market, the department maintains "oyster seed grounds" at several locations along the Louisiana coast. These seed grounds are in areas where historically there has been a good reproduction of oysters. These areas are opened to lessees and they are allowed to harvest these young oysters and transplant them to their own leases for growth to marketable size. The department maintains remote facilities staffed 24 hours a day at the major seed grounds to protect those areas from uncontrolled harvest.

There are almost 2 million acres of public reef/seed grounds, although only a relatively small portion of this area has the hard bottom substrate necessary for the existence of oysters. These public reefs are opened each year in the fall and winter both to lessees who may wish to transplant oysters to their leases and to other fishermen who may wish to harvest oysters and bring them directly to market. Each year in the summer, biological samples (Figure 3) are taken on these reefs and the results used to make recommendations as to opening and closing of areas to harvest and to advise the oyster industry on the availability of oysters on these reefs.

3. *Shell Plants.* Periodically the Department spreads large amounts of clam shell on the seed grounds for young oyster larvae to set on. Since 1926, the State has planted over one million pounds of cultch material on public seed grounds and reservations to create new reef areas or increasing production on existing reefs. In the late 1950's and early 60's reef oyster shell dredged from relict reefs along the central Louisiana coast was used to supplement steam plant shell. Clamshell (*Rangiacuneata*) has been the preferred cultch material since the mid 1960's due to its availability and because it generally produces well-shaped oysters that require minimal culling.

Clamshell is dredged hydraulically from vast deposits in Lake Pontchartrain, loaded onto flush deck barges, and transported to the seed grounds. The

Figure 3. Meter square sampling for oyster densities on the "Public Grounds".

shell is planted (Figure 4) using a specially designed "spray barge" with a high-pressure water pump with four to six nozzles.

The selection of a cultch plant site depends upon the suitability of the bottom and the anticipated salinity conditions. The bottom must be of sufficient firmness and stability to prevent the cultch material from sinking or being buried, and salinities should be within the range previously described as optimal for seed production.

Successful shell plants in Louisiana have had cost: benefit ratios as high as 20:1. Unfortunately, the cost of clamshell is escalating rapidly. Research is underway to find suitable substitutes for clamshell and to more precisely identify the environmental conditions associated with successful plants.

4. *Tags*. Legislation has been enacted requiring all oysters entering commerce to be tagged (Figure 5) with information as the location of harvest and the date harvested. This legislation has originated within the federal Food and Drug Administration. This information ensures both the quality of the oyster and enables authorities to trace shipments which do not meet public health standards. The department provides standard tags to the industry at cost; it also inspects shipments at the dock and in transit to insure that all sacks of Louisiana oysters are tagged.
5. *Health Department Closures*. Over 250,000 acres of suitable oyser habitat are now closed to harvest because of pollution. The areas to be closed are determined by the Department of Health and Hospitals (DHH) however this subprogram interacts with DHH in making that decision; the department publishes the closure decisions and patrols the closed areas to prevent harvesting from these areas. The subprogram also supervises the transplantation by leases of oysters from polluted areas to open areas. In 1986, 140 such moves were regulated. This overall State Shellfish Sanitary Program comes under the close scrutiny of the federal Food and Drug Administration utilizing guidelines established by the Interstate Shellfish Sanitation Conference (ISCC). The ISCC is comprised of both producing and receiving states, and the Department of Fisheries serves a very active role.
6. *Oyster Complaints*. This subprogram provides technical assistance to oyster lessees who believe that oysters on their leases have been detrimentally affected by oil & gas exploration and production activities, transportation activities, the activities of other

Figure 4. The deposition of cultch (clam shell) material on the "Public Grounds".

Figure 5. Tagging oyster sacks prior to entering into commerce.

fisheries, or by adverse environmental changes. Upon request by the lessee, a biolocial team will assess the condition of the oysters on his lease, will determine if these oysters have been adversely impacted, will attempt to determine the cause of any damages found, and will testify as an expert witness in court. These services are provided at not cost to the individual lessee. The decline in oil exploration has limited the number of oyster complaints for the 1986–87 fiscal year.

Many of these coastal zones' project permits have been reviewed and perhaps altered or even rejected by the Department's Permit Section. This is a section composed of eight employees to screen permit proposals and then comment to the Department of Natural Resources, and oversee Seismic operations in the coastal area as well as the state.

7. *Management Recommendations*. The subprogram devotes considerable resources to monitoring the public reefs and seed grounds. In addition to collecting production data from the seed grounds, personnel are active in collecting other biological as well as hydrological data. Spat (young oysters) set is monitored to assess reproduction success. Oyster mortality and size distribution on specific reefs are monitored by a series of dredge samples which are taken monthly. Hydrological readings are taken to document both short-term and long-term changes in water quality, which may affect the oyster production on the seed grounds. The information gathered is analyzed and recommendations are made concerning the opening and closing of seasons and areas.
8. *Controlled Freshwater Diversion*. The State has long realized the disastrous effects of saltwater intrusion on the productivity of the seed grounds and also the potential value of freshwater diversion. In 1958 a freshwater diversion structure was built at Bayou Lamoque to supply Mississippi River water to a portion of the seed grounds (Figure 6). The structure has been highly successful in increasing seed production, but its area of influence is relatively small due to the limited capacity of the structure and the circulation pattern of the region which tends to carry the freshwater away from the seed grounds.

The U.S. Army Corps of Engineers has proposed a comprehensive plan for large-scale controlled freshwater diversion from the Mississippi River to the estuarine areas of southeast Louisiana. Benefits to be realized from diversions include reduced coastal erosion, preservation of fresh and brackish

Figure 6. A controlled freshwater diversion structure located on the lower Mississippi River.

water marshes, and general enhancement of fish and wildlife resources. Seed oyster production will increase dramatically due to the establishment of favorable salinities over vast acreages of formerly productive reefs. The magnitude and timing of the diversions will be controlled to create salinity conditions similar to those which occurred during years of highly successful oyster set. An elaborate monitoring

Figure 7. Louisiana enforcement agents.

program has been established within the Department to oversee the project and its effects.

9. *Enforcement.* Once managerial decisions and laws have been passed their success is ultimately dependent on a successful enforcement effort. This becomes a truely monumental task in coastal Louisiana because of the vastness of the area. This is accomplished by some 45 agents (Figure 7) and their equipment dispersed along the coast. They are assisted by some 35 additional employees assigned to permanent facilities in the coastal areas, along with two large offshore vessels and crew, and some four aircraft to canvass the coast.

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MANAGING PUBLIC OYSTER REEFS: TEXAS EXPERIENCE

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ABSTRACT In recent years the Texas oyster harvest has tended to increase in quantity and value, comprising a larger percentage of the total U.S. landings. There has been concern that the public reefs cannot continue to support a large fishery. A transition from management by the legislature to management by the Texas Parks and Wildlife Commission (TPWC) has been underway. The TPWC has closed the oyster season several times in the past few years. In August 1987, the 1987–1988 season was closed because data from a relatively new sampling program indicated that market oysters were too sparse for harvesting without risking depleting public reefs. Oystermen, however, believed that there were ample oysters for havesting and that oystering would cease before stocks were endangered. A group of oyster dealers and fishermen filed suit against the Texas Parks and Wildlife Department (TPWD) in December 1987. The judge ruled in their favor and ordered the immediate opening of the season—thus creating an adversarial position between oystermen and the TPWD. The Texas Legislature mandated that the TPWD develop an oyster management plan that would consider socio-economic impacts as well as biology and law enforcement. If such a plan had been in effect in 1987, conflicts between oystermen and the TPWD might have been reduced, if not eliminated. We offer several suggestions for consideration in developing an effective management plan. Basically, they stress the need for input from oystermen and dealers as well as from the scientific community.

KEY WORDS: Texas, oyster management, conflicts

INTRODUCTION

In the not-so-distant past the Texas oyster industry was a minor operation, more of a part-time activity between shrimp seasons. In recent years, however, Texas oyster production has been increasing, ranging from 1–2 million pounds in 1979–1981 (Calendar years) to an excess of 5 million pounds in 1982–1986 (except for 3.6 million pounds in 1982, a transitional period). Since 1983, Texas oysters have comprised about 12 percent of the total U.S. landings compared to 3 percent during 1977–1983.

The increased harvests have concerned the Texas Parks and Wildlife Department, the agency entrusted with the management of the oyster fishery. The Texas Parks and Wildlife Commission has closed the oyster harvest in one or more bay systems several times since 1978. In 1987 the TPWC attempted to close the oyster season along the entire Texas coast, the first time total closure was ever imposed.

In 1985, the authority to regulate the Texas oyster fishery was granted to the Texas Parks and Wildlife Commission by the sixty-ninth Texas Legislature. Thus by this action the Texas Parks and Wildlife Commission could regulate by proclamation rather than by statute. However, the Legislature required that an Oyster Fishery Management Plan as well as an Economic Impact Statement be developed by the Texas Parks and Wildlife Department (TPWD) before existing regulations could be changed. Also, the 1985 Legislature provided for a Joint Interim Committee on the Texas Shrimp and Oyster Industry to assist with development of this plan. The term of the Interim Committee expired January 1987 and it played no role in the development of the proposed plan.

HISTORY OF MANAGEMENT OF PUBLIC REEFS

Historically the Texas oyster fishery has been managed by the state legislature through statutes which tend to restrict the catch from public reefs. Such restrictions include: a season (November 1 through April 30); time of day (sunrise to sunset); size limit (3 inches); cargo limit (50 bbls.); and gear restrictions (one dredge not more than 48 inches in width). Other legislation regulates culling and the scattering of culls. In addition, the Texas State Health Department establishes the approved and unsanitary oystering areas. Over many years these regulations have usually been sufficient to allow uninterrupted harvest seasons without damaging the oyster resource.

The legislature has also given the Texas Parks and Wildlife Commission (and its predecessors—the Texas Game, Fish and Oyster Commission and the Texas Game and Fish Commission) the authority to plan and implement various management programs. Such management has not necessarily been restrictive. During the 1950s power dredging was permitted in waters over 3 feet deep (rather than being limited to waters over 6 feet deep). This increased the harvests in many bay areas which had been off limits to dredge boats. In 1963 the legal size limit was reduced from 3½ inches to 3 inches based upon studies that showed there was a sharp increase in mortality among oysters over 3 inches in size (Hofstetter 1977). Shell plantings were made in several bay systems over an ex-

tended period to increase the acreage of harvestable reefs or to enhance the recovery of flood-damaged reefs (Crowe and McEachron 1986).

CLOSURES OF THE TEXAS OYSTER FISHERY

The Commission has also had authority to close an area to oystering if it is in danger of becoming depleted. Such closures have been infrequent in past years. During the 1950s and early 1960s, several bay areas were closed during part of a season. Most closures applied only to power dredging, allowing shallow water reefs to remain open for hand dredges and tongs.

Closures were based, in part, upon data obtained by monitoring oyster populations in several bay systems. Periodic samples were collected at fixed reef stations within each bay system. One bushel of oysters was dredged at each station and all live oysters were measured and counted. By the 1970s, oyster sampling had been discontinued in all systems except Galveston Bay where oyster harvests were concentrated. Beginning in 1976, to provide more information on the quantity of oysters available to the oystermen, timed samples were collected at major harvest areas prior to the opening of each season. Five one-minute dredge hauls were made at each station and all market size oysters were counted. Timed samples were repeated periodically during the open seasons to detect changes. Later, pre-season timed samples were collected in four other bay systems. Neither the standard bushel sample nor the timed sample indicate the actual number of oysters per unit area. However, over time, they furnish information on trends in abundance of seed and market oysters at established stations.

In 1978, following three successive years of poor spat sets, the number of market oysters in pre-season samples at Galveston Bay stations was very low (averaging 24 per 5 minute dredge haul). Although the season opened as usual, the number of working boats dropped from about 30 to less than 10 within a week. Because market oysters were scarce but spat had become plentiful, the Commission closed Galveston Bay on December 15 (after a 45 day season). This was done to allow the young seed oysters to grow. But it was also done because most of the oystermen wanted the bay closed. Other Texas bays remained open. The opening of the 1979–1980 season was delayed 45 days to allow oysters to recover from the effects of torrential rainfall in late summer. A bay-wide spat set of major proportions occurred in 1980, leading to substantial harvests in 1981 through 1983. No closures were necessary during these years.

Somewhere along the way, the mean number of market oysters in the 1978 timed samples (24) became the official depletion level. If market oyster numbers appeared to be approaching that level, action would be taken to stop harvesting altogether. During the 1983–1984 season the Commission became alarmed over the large number of out-of-state boats in Galveston Bay. Timed samples were ordered to be collected weekly and the "market count" reported to the Commissioners. The Commission decreed that the bay would be closed when that count dropped to 30. This occurred in March 1984 and the season in Galveston Bay closed one month early.

Beginning in October 1984, the oyster sampling program in Galveston Bay was changed from the fixed station to a random grid sample (Benefield et al. 1986). Initially 80 reef grids (and 20 "non-reef" grids) were sampled monthly. Later, the number of reef grids was reduced to 56. At each sample station a 30-second dredge haul was made. Nineteen randomly selected oysters were measured and the remainder counted. Spat abundance was determined by counting spat on one side of each of five live oysters and five dead shells (with the remaining dead shells counted). These figures were used to calculate the number of spat, small oysters and market oysters in each sample. Since the Commissioners had become familiar with the old "count" figure derived from the 5 minute sample, the 30-second sample data were converted to a corresponding "market count" simply by multiplying by ten. Beginning in 1986 random grid oyster sampling was expanded to include all other bay systems and, when requested, a "market count" was provided to the Commissioners.

In August 1987 data from this new- and untested-sampling program indicated that the count in almost all bay systems was near the official depletion level. Staff projections suggested that the reefs would not be able to support a harvest by November 1. The Commission, following staff recommendations, ordered the oyster season closed along the entire Texas coast until further notice.

MANAGEMENT CONFLICTS

Oystermen, although agreeing that market oysters would not be abundant, contended that harvesting would not lead to depletion. They believed oystering would cease long before the reefs were endangered. Moreover, they were suspicious of the new random sampling method and the 30-second dredge sample. They believed that samples from non-productive or marginally productive reefs (where oystermen would not normally work) were averaged in with better samples, tending to lower the count. They did not believe a 30-second drag with the small sample dredge could collect an adequate sample.

In spite of protests expressed at the August 1987 Commission meeting, the season did not open on November 1. However, a group of oyster dealers and fishermen filed suit against the TPWD in December 1987. The judge ruled in their favor, ordering an immediate opening of the oyster season. Thereafter, the Texas oyster season proceeded to the normal closing date (April 30, 1988). Although relations between oystermen and the Texas Parks and Wildlife Department have not always been cordial, this issue has exacerbated an adversarial relationship between the two.

We do not believe such a relationship is in the best interestes of either party.

The TPWD has been mandated by the legislature to develop an oyster management plan considering socio-economic impacts as well as biology and law enforcement. Although preliminary hearings were held over two years ago to obtain public input, a draft plan was not made available to the former Interim Committee members and the public until late August, 1988. A workable plan would have reduced, if not eliminated, the conflicts created in the 1987–1988 season.

CONCLUSIONS AND RECOMMENDATIONS

An agency responsible for administering a workable plan should have comprehensive knowledge of the industry it is to regulate. Admittedly, the Texas oyster industry has, and remains, fragmented, with no major voice to speak on its behalf. More often than not, the TPWD has received conflicting signals as to what is, or is not, desirable. Input from oystermen and dealers is essential if a management plan is to succeed. In addition a management plan should be subject to scrutiny by knowledgeable scientists outside the agency. Texas oysters have provided a larger portion of the total U.S. output and there will be considerable out-of-state interest in how the state plans to manage its oyster resource. There is an opportunity to make the Texas plan a model for others. This opportunity should not be lost because of mistrust between the industry and the regulatory agency.

Since both of us have been involved, directly or indirectly, with management of the Texas oyster fishery, we feel qualified to offer the following suggestions for consideration in the management plan.

1. Management should be flexible. Regulations proposed at the beginning of a season need not be set in concrete. Flexible seasons with delayed openings in selected bay systems might be appropriate.
2. By all means involve dealers and fishermen in management options. These might include sack limits, size changes, shortened harvest days, etc. which could allow limited harvesting when oysters are scarce.
3. Oystermen should be participants in pre-season samplings. "Field days" when oystermen could sample reefs with their own equipment might be incorporated into the management plan. But sampling data should be readily available to the oystermen and dealers. Such data might be more relevant if reported as number per hour or sacks per hour.
4. Oystermen should participate in maintaining, or expanding, oyster reefs. Shucked shell from oyster houses could be used to build new reefs or enlarge old ones. But care should be taken in selecting sites for shell plantings. Galveston Bay, the major oyster harvest center, should be given preference.
5. Basic biological studies should not be neglected. Because poor spat sets have become frequent, studies of larval source, distribution and survival appear to be necessary. Effects of predation and disease upon both public and private beds are poorly understood.
6. Qualified scientists within (and without) Texas may be willing to advise on management or research problems. Several might be enlisted to serve as an advisory board to TPWD.
7. The concept of oyster depletion based upon sample dredge counts should be re-assessed. No evidence has been presented to show that depletion occurs if the market oyster count reaches 24. Commercial gear might be more appropriate in assessing the abundance of oysters.
8. Although interest in private oyster leases remains high, the TPWD has imposed a moratorium on leasing (since 1986). But oyster leases—in appropriate areas—should be encouraged. Through proper leasing, submarginal bottoms are enhanced by transplanting oysters from closed areas; oysters that would otherwise be lost to the harvest (or harvested illegally).
9. In more saline areas, consideration should be given to the culture of species other than the oyster (such as hard clam). Provision for private culture and harvest should be made.

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OYSTER HATCHERIES ON THE GULF COAST: HISTORY, CURRENT TECHNOLOGY AND FUTURE TRENDS

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ABSTRACT The early history of oyster culture is discussed through the development of hatcheries in the Gulf of Mexico. The development of the brown water culture method is presented. Various setting studies were conducted with the following results: setting in the hatchery was best on washed oyster valves, but in the wild, green shell caught more spat than did aged shell, attempts to produce a coated cultch were unsuccessful, and in the hatchery, clam shells were found to be the preferred substrate when compared to three other substrates. Loss of larvae to setting on tanks is discussed. Various other studies showed that: optimum fertilization was 75 sperm per egg, spat did not survive planting in mud, predation on cultchless oysters occurs throughout most of the year and is size dependent, and blue crabs can open oysters 40% their size. Spat set on shucked shell survived up to a week air drying and grew 2.9 mm/mo after replanting. Growth of cultchless spat in five systems varied from 1.2 mm/mo. to 3.3 mm/mo. Future trends toward land based aquaculture are discussed.

KEYWORDS: oysters, hatchery, setting, history

INTRODUCTION

Interest and research in oyster culture is inversely related to the cycle of natural oyster production, however, the trend has been for a decline in total production. Concern over declining production has been expressed since the turn of the century. Historically, the Gulf of Mexico has been an area of high oyster production with an abundant spat set, but in recent years set failures in Texas (1976–1977), Louisiana (1977–1978) and Mississippi (1978–1979) have shown the need for development of oyster culture technology. The use of a brown water technique for operation of hatcheries provides the opportunity for individual oyster farmers or cottage level industries to develop in the Gulf of Mexico. Even though producing larvae is now not a problem, there is a lack of technology to set the larvae on a commercial scale. The future of oyster culture is projected to be a land-based aquaculture because at present there is a lack of technology and social attitude conducive to oyster farming in the public waters of the Gulf of Mexico.

This paper will discuss the development of oyster hatcheries in the United States, including all known hatcheries in the Gulf of Mexico. The current technology used by Gulf hatcheries will be reviewed. Original data on setting is presented and previously reported data on survival, predation, and growth will be reviewed. Finally, some trends will be projected for the future.

HISTORY OF OYSTER HATCHERY TECHNOLOGY

Oyster culture is not new. Aristotle, in 320 B.C., came to the conclusion that oysters grew from mud by spontaneous generation. The first oyster beds are thought to have been laid out by a Roman, C. Serguis Orata, in 97 B.C. Orata was also the first oysterman to be involved in a dispute over lease rights. Ausonius, in the latter half of the fourth century, described suspension culture of oysters (Gunther 1897). The reluctance to eat oysters during months lacking an r in their name is attributed to a man named Butler in 1599 (Hedeen 1986). The first "act for the preservation of oysters" in the United States was enacted in 1766. The first transplantation of oysters occurred in 1810 and the shells were first planted to catch spat in 1855 (Galtsoff et al. 1930).

Seven years before Brooks (1879) described the larvae of the American oyster, a patent was issued for an improvement in oyster nurseries (Lyford 1872). Ryder (1883) described a system for the cultivation of oysters utilizing a pond, and Walton (1891) was granted a patent for an even more elaborate apparatus for oyster culture consisting of conduits, pipes and tanks. Prytherch (1924) reported on the use of a porus stone he called filtros to produce oysters. Elsworth (1926) received a patent for a hatchery for marine life which relied on intersecting the tidal flow and utilized fixed screens, rotating screens and a centrifuge for purifying the water. Although Wells began producing oysters in a hatchery in 1919, his patent was not granted until 1933 (Wells 1933). Generally considered to be the first successful oyster hatchery, he utilized a centrifuge to first remove the large predators from the water and then to remove the oyster larvae so they could be placed in new water. Walne, working at Conway during the period 1919 to 1935, perfected the production of oysters in large seawater ponds. The use of fertilizers to promote phytoplankton production was investigated during the period 1936 to 1961 (Walne 1974). Pure cultures of a phytoflagellate was accomplished by Miquel (1890–92) and a suitable pure culture of marine flagellates for oyster culture was first available in 1936 (Walne 1974). In 1930, oysters were successfully reared on a defined diet of *Fucus* antherozoids, and

oysters were first reared on an algal diet in 1940 (Walne 1974). In 1945, the American oyster was first conditioned for out of season spawning (Loosanoff 1945) and in 1953, a suitable algal diet was developed (Davis 1953). Glancy (1965) was granted a patent for a method for raising shellfish seed in a simulated habitat. His patent provides for removing predators and silt by centrifuging growing water, providing for solar radiation by the use of a greenhouse, and providing smooth walled tanks and constant aeration for the larvae. The patents of Budge provide for production of cultchless oysters (Budge 1970a), upwelling nurseries (Budge 1970b) and remote setting (Budge 1973). Today the term "Wells-Glancy" is used to describe the production of oyster larvae utilizing a centrifuge to coarsely filter bay water which is fertilized and allowed to bloom. The use of pure cultures of known algal species which are fed at controlled rates to larvae is generally referred to as the "Milford" method of culture. A third system directly utilizes natural growing waters which have only been filtered through inexpensive bags and has been referred to as the "brown water" method (Ogle 1982).

In the Gulf of Mexico, the first shellfish hatchery was that of Menzel working at Alligator Harbor, Florida in 1960 where small quantities of algae were used to rear clam larvae in fingerbowls on a laboratory table. The lab was moved to Turkey Point, Florida in 1965 and the work was continued until 1980 (Menzel pers. comm.). Ray, in 1970, attempted to establish an oyster hatchery at Cedar Bayou, Texas but several years of excessively fresh water precluded any success (Ray pers. comm). In 1975, the Louisiana Department of Wildlife and Fisheries (LDWF) personnel at Grand Terre, Louisiana were operating a laboratory scale hatchery utilizing the "Milford" method. In 1975, the Mississippi Marine Resources Council funded the Gulf Coast Research Laboratory (GCRL) for the construction of a 148 m^2 (1600 sq. ft.) pilot seed oyster hatchery to be constructed at Point Cadet in Biloxi, Mississippi. The facility originally intended to use a "Milford" culture method and produce cultchless oysters but developed the brown water method in 1977 and produced cultched oysters until 1985. In 1980, the LDWF began construction of a 49 m^2 (525 sq. ft.) brown water hatchery at the Lyle St. Amant Marine Research Laboratory, Grand Terre, Louisiana which has operated since 1981. In 1984, larvae from that hatchery were remotely set in tanks and on commercial oyster leases (Scarborough-Bull and Cole 1985). In 1987, Ray constructed a brown water hatchery in Offats Bayou, Galveston, Texas. A private oysterman in Louisiana has even operated a brown water hatchery system on his boat (Peter Vujnovich pers. comm.).

CURRENT HATCHERY TECHNOLOGY

The production of oyster larvae is no longer a problem to the industry. The brown water hatchery can be put into place easily and inexpensively and has been shown to be a viable concept in Mississippi, Louisiana and Texas. A description of the method can be found in the publication of Ogle 1982. Briefly, the system consists of raw bay water pumped into 1892.7 l (500 gal.) tanks after being coarsely filtered through 5 m bags to remove predators and competitors (Fig. 1). The water is changed every three days, and there is no need for supplemental food as this system is dependent on nutrient rich natural seawater. The tanks were covered with a "greenhouse" although it is not necessary. The plastic house was the least expensive means to cover the tanks to prevent rain from diluting the salinity. Out of season conditioning was not successful. However, sources of oysters were found that could be spawned every month except January and February even though there is still ample food present in the water (Ogle 1979). Oysters were difficult to spawn during July and August because the high summer water temperatures made it difficult to thermally shock the oysters. It was possible to hold oysters under cooled bay water into the summer and under heated water into the winter and achieve better spawning. In addition, it was sometimes possible to achieve better spawns during the warmer summer months by holding the oyster for several days in the refrigerator. Utilizing brood stock from low salinity areas, it was possible to rear larvae at salinities as low as 7 ppt. However, artificial sea salts were used to adjust salinities to at least 10 ppt during times when the salinity of the incoming bay water was low. Brine (70 ppt) produced from a solar evaporator was also demonstrated to be effective. In Louisiana, a narrow range of salinity (12–17 ppt) is associated with natural seed production (Chatry et al. 1983).

Although it was determined that 75 sperm per egg was optimun for fertilization (Table 1) in normal operation, sperm were not counted but instead a small amount of sperm suspension was used to avoid over fertilization. The GCRL hatchery was not operated full time (Table 2). Production decreased initially due to bacteria building up in the

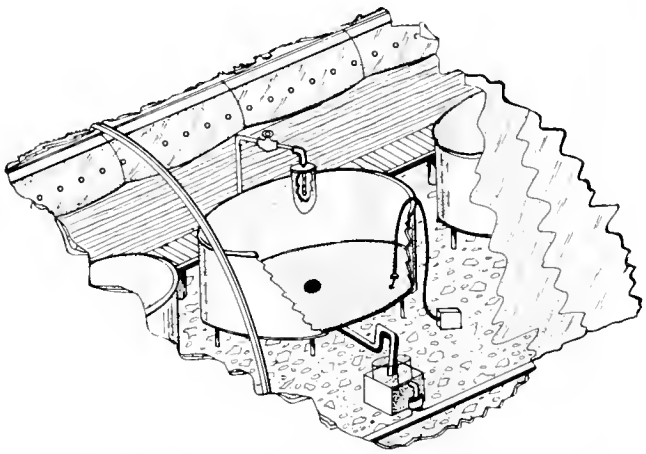

Figure 1. Diagramatic representation of facility used in "brown water culture" hatchery for *Crassostrea virginica*.

TABLE 1.

The effect of various sperm to egg ratios on the % fertilization of *Crassostrea virginica*.

Sperm/egg	Eggs/ml 30	50	50	50	Average
50	67%	36%	—	40%	47.6%
75	71%	40%	60%	44%	53.8%
100	46%	29%	—	41%	38.6%
150	—	24%	23%	31%	26.0%

TABLE 3.

Spat set per oyster valve under wild and hatchery conditions and with valves boxed or bagged.

	Wild		Hatchery	
	Bags	Boxed	Bags	Boxed
# valves	94	178	71	186
# with spat	2	2	68	180
# spat	2	2	723	2955
% shells with spat			95.8	96.8
spat/valve			10.6	15.9

algal cultures and in the water systems while the hatchery was operated on a "Milford" system. An attempt to utilize the Wells-Glancy method by fertilizing the bay water was not successful. The larvae were probably killed by the excess nitrate added to the water as there is sufficient nitrate in the incoming water to support the algae. Production increased dramatically once the brown water technique was begun. Larvae can be set on cultch or cultchless.

Despite the issuance of a large number of patents dealing with setting oysters and producing spat, no field technique has been demonstrated to be effective for the handling of cultchless seed. At the GCRL hatchery, cultchless seed were produced utilizing sheets of mylar plastic folded into boxes to prevent larvae from setting on the trays. Some of the larvae were lost when they set on the culture tanks or on containers. On several occasions, all the larvae were "lost" when they set in the beaker while being carried to the setting tanks. Attempts to duplicate this behavior on demand by physical, temperature or photic shock were not successful. Silicone, teflon, waxed or vaseline coatings did not deter setting of the larvae on the sides of the tanks. Overall, 21.3% of the larvae were lost to the tanks, 35.7% were lost to the trays holding the substrates and the remaining 43% were set on substrates. Setting on whole oyster valves was not affected by whether the shells were in bags or boxes, even though the boxes (milk crates) held over twice the number of shells (Table 3). In the hatchery, aged, washed shell caught almost three times as many spat as did aged, unwashed shell and almost 16 times as many spat as green shell (Table 4). However, in the wild, the green shell caught more spat than did any of the other shells. Green shell used in the hatchery quickly fouled the water. In a subsequent study on rebedding green shell, 78% of the shells caught an average of 3 spat per shell. Results from three trials of four different substrates for setting preference were mixed (Table 5). Dolomite was the least preferred and clam shell the most preferred substrate. The same substrates placed in the wild caught no set during 1979 when this study was conducted. During the same period, bagged oyster valves in the wild caught only 1 spat per 80 shells. Attempts to coat substrates to improve their ability to catch spat were not successful. Combinations of mortar mix, topping mix, blockfill, hydraulic cement and lime would not stick to plastic bread trays or orchard netting even when mixed with seawater, salt, or glue. Snow white finishing lime provided a marginally acceptable coating. The problem of how to handle the large numbers of oysters that can be produced from hatcheries still remains. Shell must be washed, contained and offered to the larvae in a single layer and cultchless spat must be protected from predation and siltation. Mortality of cultchless spat planted in mud after 6 months was 100% for small spat (23 mm) and 80% for spat (47 mm), whereas only 27% of the spat planted in trays died. Blue crabs are known to be able to open oysters 40% their size (Ogle 1978). Predation on unprotected cultchless seed occurs every month except January and February for 20 mm spat. For 30 and 40 mm spat, predation occurs from April until October and for 50 and 60 mm spat, predation occurs from June until September (Ogle 1980).

Growth of spat was found to vary with location from 1.9

TABLE 2.

Summary of production over a six year period for the G C R L hatchery in terms of time operated, broods, larvae and set.

	Period of Operation	No. of Broods	No. of Day 1 Larvae	No. of Eye Larvae	Larval Mortality	No. of Larvae Set
1975	Aug–Nov 4	6	5×10^6	—	—	200
1976	Mar–Oct 8	16	94×10^6	15×10^6	84	32,814
1977	Apr–Oct 7	11	43×10^6	1×10^6	99.4	4,145
1978	Apr–Oct 7	11	138×10^6	7×10^6	94.6	279,277
1979	Jul–Aug 2	6	56×10^6	20×10^6	64.3	—
1980	Jul–Aug 2	5	81×10^6	15×10^6	81	—

TABLE 4.

Effect of washing on ability of green, aged and washed oyster valves to catch spat under wild and hatchery conditions.

Planted	Spring–April–1978			Fall Oct. 1978	Hatchery 1978
Duration	2 mo. June	6 mo.	9 mo.	3 mo	
Freshly shucked (green)					
# of spat	13	47	83	5	797
# valves with spat	12	29	49	4	85
# valves without spat	82	67	51	96	4
% catching	12	30	49	4	96
spat/valve	0.13	0.49	0.83	.05	8.95
Aged (dried)					
# of spat	22	58	85	1	2408
# valves with spat	17	36	46	1	50
# valves without spat	83	62	59	99	0
% catching	17	37	44	1	100
spat/valve	0.22	0.59	0.80	.01	48.16
Washed					
# of spat	8	40	46	4	5537
# valves with spat	7	35	34	3	39
# valves without spat	93	71	67	97	0
% catching	7	33	34	3	100
spat/valve	0.08	0.38	0.46	.03	141.97

to 3.3 mm/mo (McGraw 1980). Growth was not significantly different between hatchery singles, wild singles or cultched hatchery seed (Table 6). Growth in five different systems of culture at the Biloxi Bay site was generally poor, ranging from 1.19 to 2.26 mm/mo, although some treatments achieved growth rates of 4.15 mm/mo (Ogle and Beaugez 1988). Growth of spat surviving on shucked green shell that were replanted was 2.9 mm/mo (Ogle and Chestnut 1979), with 31% of the spat recovered and 9% surviving. Survival of spat on shucked shell left dry for 10 days was 17% while over 40% (40 to 45%) of spat left dry for period from two to nine days survived. In laboratory studies, cultchless spat 10 mm in size survived drying for 6 to 8 days at temperatures ranging from 15° to 30°C. At 30°C, spat ranging in size from 10 to 50 mm also survived for 6 to 8 days.

FUTURE

It is ironic that as oyster production declines due in part to environmental stress from flood, drought, saltwater intrusion and disease, the environment provides a means of producing larvae inexpensively in hatcheries. It should also be noted that since low technology hatcheries have been shown to be feasible, high technology chemical hatcheries have also been developed. The use of serotonin to induce spawning, cytochalasin B for producing triploid oysters and epinephrine for inducing cultchless setting is an interesting contrast to the use of brown water for producing spat. Remote setting, especially as demonstrated in Louisiana (Scarborough-Bull and Cole 1985) by releasing eyed larvae into the wild on commercial leases, is certainly an interesting concept. With the exception of Louisiana, private leasing for culture of oysters has not been widely practiced in the Gulf of Mexico. Recent interest by oystermen in hatchery production to counter declining production and lack of sets is encouraging. In addition to changing attitudes of the oystermen, there is new interest in culturing oysters as a land based aquaculture crop. The emergence of an economically viable shrimp farming industry in Texas and South Carolina has led to a renewed interest in pond

TABLE 5.

The effectiveness of four substrate types to catch spat under hatchery conditions.

	Percent Setting		
Substrate	Trial 1	Trial 2	Trial 3
Shell hash	4.5	7.8	67.7
Dolomite	14.2	26.7	7.6
Crushed shell	41.8	6.7	5.3
Clam shell	39.4	58.8	19.4

TABLE 6.

Average growth rates of cultchless hatchery reared spat in varying systems.

System	Number Experiments	Growth mm/Mo.
Flume	6	2.26
Tank	1	1.19
Suspended	1	1.78
Off bottom	1	2.09
On bottom	1	2.90

aquaculture of oysters. With a decline in oystser production from the East Coast, the Gulf of Mexico has become the leading oyster producing region. However, the consumption of oysters has increased leading to increased imports of oysters. The deficit in trade, available technology, a declining fishery and innovation of the watermen offer an excellent opportunity for oyster aquaculture if the social and legal obstacles can be dealt with.

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OIL AND OYSTER INDUSTRY CONFLICTS IN COASTAL LOUISIANA

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ABSTRACT The juxtaposition of the oil and oyster industries in coastal Louisiana has led to inevitable conflicts. Chief among these problems are the sedimentation and burial of oysters due to dredging or other operations. (Oil spills are relatively rare events.) Methodologies for the assessment of damage include "before-and-after" surveys which evaluate oyster mortality and habitat alteration. A system of compensation has evolved in which oystermen, who lease the waterbottoms from the state of Louisiana, are paid for damages due to oil and gas activities. In a recent Louisiana Supreme court case, the court discarded the established negligence standard and adopted a strict liability approach. The established negligence standard held that the mineral lessee is not liable to an oyster lessee for damage resulting from necessary and prudent operations conducted with reasonable skill and precaution, whereas the strict liability approach has made the mineral lessee liable for any operations which damage oyster property.

KEY WORDS: oysters, *Crassostrea virginica*, Louisiana, policy, management, surveys

INTRODUCTION

Louisiana is the nation's leader in oyster production and coastal petroleum development. Nowhere else in the world do the oil and oyster industries come into greater conflict than in the shallow bays and meandering bayous of coastal Louisiana. Although the two industries are not mutually exclusive, inevitable conflicts arise as they exploit their respective resources.

The purpose of this paper is to review the history of the conflict, highlight methodologies for the assessment of damage, examine oil and oyster leasing policies, discuss legal aspects of the problem, and evaluate the question of adequate compensation.

HISTORY OF THE CONFLICT

Oystering in Louisiana was conducted long before 1886 when the first oyster lease law was enacted (Cake and Dugas 1986); the first oil production in the coastal zone occurred in 1926 (Franks and Lambert 1986). Annual oyster harvest (from 1923 to 1986) has varied from about 3 to 14 million pounds of meat, whereas oil production from south Louisiana (1925 to 1986) has ranged from about 3 to 366 million barrels per year (Figure 1). Thus, while oyster harvest has varied by a factor of less than 5, oil production has varied by more than two orders of magnitude. In good years today, as many or more oysters are harvested than in the pre-oil era (although with more effort applied). Variations in oyster production are largely determined by salinty fluctuations, and to a lesser extent by fishing effort.

The rapid expansion of the oil industry in coastal Louisiana just prior to World War II brought the industries into sharper conflict. Numerous lawsuits claiming damage to oysters due to oil operations were filed. A particularly significant case was *Doucet vs. Texas Company* [205 LA 312, 17 So. 2d 340, La. 1944] in which (upon appeal) more than $200,000 was awarded to the oysterman (Reese 1954). More litigation followed. The Texas Company (now called Texaco) contracted with the Texas A&M Research Foundation to determine if oil activities were harming oysters. Other oil companies joined the Texaco effort and the largest study of oyster biology was initiated (Hopkins 1980).

Extensive studies were conducted on the effects of crude oil, bleedwater, natural gas, drilling mud and seismographic surveys on oysters (Mackin and Hopkins 1958). The general conclusion of the studies was that none of these pollutants or activities could explain the widespread mortalities of oysters observed. The greatest contribution of the Texas A&M study was the discovery of *Dermocystidium marinum* Mackin, Owen and Collier (now called *Perkinsus marinus*), the causitive agent of significant oyster mortalities on the Gulf and Atlantic coasts (Mackin, Owen and Collier 1950; see also Reese 1954, Anonymous 1956a, 1956b, Sparks 1984).

Conflicts between the industries continue today, but are typically focused on a smaller set of issues. Most complaints by oystermen relate to siltation and burial of oysters. Oil spills, which render a crop temporarily unsuitable for marketing, are more infrequent events. Cake and Dugas (1986) investigated about 350 cases (since 1940) of oyster damage. Most (75%) were the result of dredging and siltation, some (17%) involved oil contamination of oysters (oily taste), and the remaining complaints (8%) involved miscellaneous problems (e.g., barge groundings, seismic damage).

METHODOLOGIES FOR THE ASSESSMENT OF DAMAGE

Methods for the assessment of damage to oysters due to oil and gas activities have been discussed by Mackin and Hopkins (1961) Mackin and Sparks (1961), Mackin (1961), Brodtmann (1983) and Soniat (1987). Ideally, pre-impact studies are conducted to collect "base-line" data

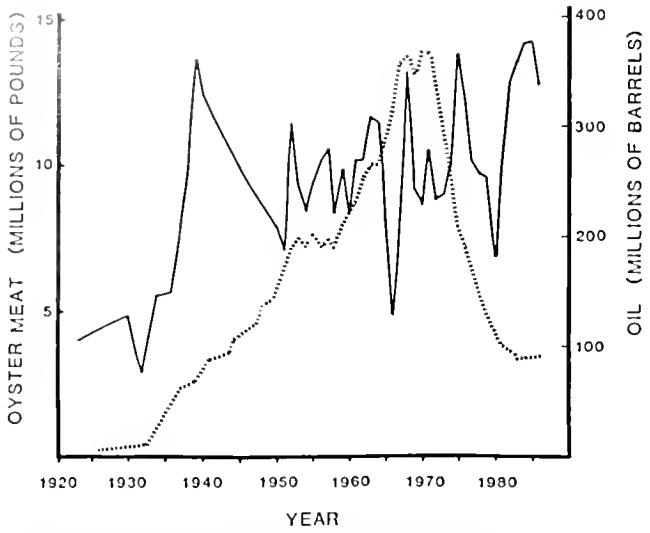

Figure 1. Graph of annual oyster harvest (solid line) versus annual oil production from South Louisiana (broken line).

that is compared to data from post-impact studies. An oyster Habitat Suitability Index (HSI) model, developed by Cake (1983) and field tested and modified by Soniat and Brody (1988), provides a conceptual framework for evaluating the effects dredging and siltation on oysters (Soniat 1987). Variables of the model are: percent of bottom covered with suitable cultch, mean summer water salinity, mean abundance of living oysters, historic mean water salinity, frequency of killing floods, substrate firmness (mean penetrometer value), density of southern oyster drills (*Thais haemastoma*), and incidence of the parasite *Perkinsus marinus*. "Before-and-after" studies which measure an HSI (or its variables) address the two central questions of oil impact studies:

1. How many oysters were killed? and
2. How was the habitat altered?

Sediment traps employed at various distances from a dredging operation (Brodtmann pers. comm.), pre- and post-impact sediment coring (Mackin 1961), and side-scan sonar (Fleming 1976) are sometimes appropriate. Dealteris (1988) found mixed results in the capability of side-scan sonar to distinguish mud bottoms from oyster reefs, although it was found useful in identifying bottom scars. In the experience of the author, side-scan sonar has been useful in identifying and locating oyster reefs, calculating reef area, evaluating sedimentation on reefs, and assessing damage due to barge and tug groundings (Figure 2). The technique is adaptable to very shallow water (4–5 ft.) by mounting the sonar transducer on a stationary boom attached to the bow of the boat.

Side-scan and general oyster damage surveys require precise positioning information. Surveyors are required to lay out sonar transects, locate sample stations, delineate hard bottom areas, and tie-in lease boundaries. Methods of surveying have progressed from stadia surveys using points of land and man-made structures as bearings, to more advanced sound surveying systems employing concrete monuments in the marsh. These improvements allow for the location of leases onto a fixed coordinate grid, as opposed to locating them in relation to semi-permanent structures and eroding points of land (Dugas 1982).

OIL AND OYSTER LEASING POLICIES

The Louisiana State Mineral Board is authorized to grant oil, gas and mineral leases on State lands, including water bottoms. A written request for advertisement, which contains a detailed description of the area, is submitted to the Secretary of the Department of Natural Resources. The advertisement must set forth the description of the land to be leased, the time and place where the bids will be received and the minimum royalty demanded. Sealed bids can be presented in person or by mail. Joint bids are acceptable. The Board has the authority to accept the bid most advantageous to the State, may reject all bids, or may lease a lesser quantity of property than advertised. (Louisiana State Mineral Board 1988).

In contrast, oyster bottoms are leased by the Louisiana Department of Wildlife and Fisheries on a first-come, first-serve basis. Lease sales are typically held once a year. Water bottoms cost $2 per acre per year, and no more than 1000 acres may be leased to a single individual. After the lease has been obtained, the Department of Wildlife and Fisheries provides surveyors, at a charge to the oyster farmer, to establish the lease boundaries (Dugas 1982). A sealed bid system should be considered for leasing oyster bottoms. It is a more orderly process and may result in a greater financial return to the State. It does tend to eliminate the "little man", yet this can be partially circumvented by allowing joint bids to be submitted.

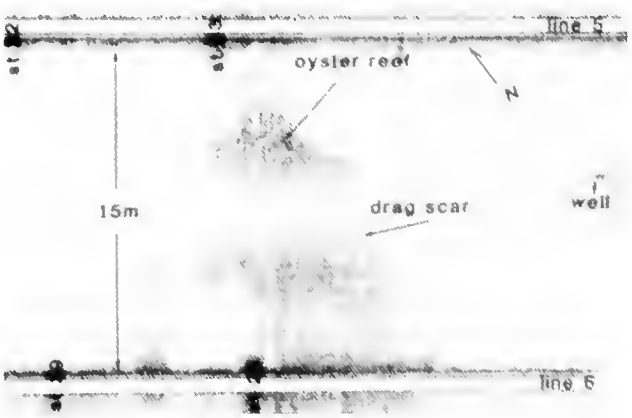

Figure 2. Photographic reproduction of a side-scan sonar record. Denser areas represent oyster bottoms, whereas lighter areas are mud bottoms. Lines 5 and 6 are transect lines. Stations are areas marked by survey poles, located by surveyors, and marked on the event recorder of the sonar apparatus. Location of a drag scar on the oyster reef, created by a grounded vessel, is indicated on the figure.

LEGAL ASPECTS

A landmark case that must first be considered is *Doucet vs. Texas Company* [previously cited]. In this case the Louisiana Supreme Court decided that, although the Statutes and leases give the mineral lease priority over a co-terminal oyster lease, the oysterman and oil company have correlative rights. The mineral lessee did not need the permission or consent of the oyster lessee to conduct mineral operations; however, the oil company must compensate the oysterman for any damage due to negligent operations. In the case of *Jurisich vs. Louisiana Southern Oil and Gas Company* [284 So. 2d 178 La. App. 4th Cir. 1973] the Fourth Circuit applying *Doucet* found that a mineral lessee is not liable to an oyster lessee for damage resulting from necessary and prudent operations conducted with reasonable skill and precaution. Thus, the more general standard of *Doucet* was specified to a greater extent in *Jurisich* (Fitzmorris pers. comm.). In particular, prudent operations require that the mineral lessee locate all oyster reefs which might be affected by its dredging, select a dredging route that minimizes damage, and notify the oysterman in advance of dredging activities.

With regard to compensation, the courts have held that the oysterman is entitled to the year of the damage plus one additional year (See *Lauzon vs. J.C. Trahan Drilling Company* [247 So. 2d 236 La. App. 4th Cir. 1971].) Although shell material for reef reconstruction has been awarded in out-of-court settlements, the so-called "reconstruction theory" of damage advanced by oyster fishermen has been rejected by federal courts in several unreported decisions (Fitzmorris pers. comm.).

In a recent Louisiana Supreme court case, *Burke vs. Progress Petroleum et al.* [no citation yet available], the court discarded the established negligence standard and adopted a strict liability approach based on Article 667 of the Louisiana Code. The article, which was intended to prevent neighbors from constructing works upon their property that would interfere with the free enjoyment of their neighbor's property, was applied to dredging and oil field work. Since the article does not require the finding of any negligence on the part of the landowner, the court in effect has made the mineral lessee liable for any operations which damage oyster property provided, of course, that the court finds a causal link between the oilfield operations and the damage to the oyster lease. The oil companies have filed amicus curiae briefs in support of rehearing this case (Fitzmorris pers. comm.).

COMPENSATION

As previously mentioned, the *Lauzon* case established that the oysterman is entitled to compensation for damages plus an additional year. However, not all compensation has been constrained by the *Lauzon* ruling, and not all damages have been compensated. For example, in a few cases, more than $1 million dollars has been awarded to oystermen (certainly more than actual damages plus one year) and out-of-court settlements that exceed actual damages are often made.

On the other hand, not all damages are compensated. The author testified in a recent case that about 4 acres of oyster bottom were harmed by a dredging operation, yet no compensation was awarded. In the absence of any use of the lease to produce oysters, the court determined that no compensation was required. The most useful record an oysterman can produce to legitimize his damage claim is information on the number of sacks of oysters produced per year on each lease.

CONCLUSIONS

As evidenced by the fact that Louisiana is the nation's leader in oyster production and coastal petroleum development, the oyster and oil industries are not mutually exclusive. Inevitable conflicts, however, have arisen as these industries exploit their desired resources. Coexistance is possible due (in part) to a system of compensation and legal guidelines. The relationship between the industries continues to evolve. Of particular significance is a recent legal ruling which discards the traditional negligence standard and adopted a strict liability approach.

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THE LOUISIANA OYSTER INDUSTRY: ECONOMIC STATUS AND EXPANSION PROSPECTS

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ABSTRACT As the nation's largest marine fisheries producer, Louisiana achieves its rank through diversity. Crustacean, mollusk, and finfish businesses are numberous and often specialized by species. Within the state's oyster industry, significant diversity exists in a diminishing coastal area. The authors delineate the production of oysters from public grounds and private leases and examine trends in landings, value, and price. These trends demonstrate the importance of Louisiana's oyster industry to that of the nation. The value-added aspect of Louisiana's oyster industry was analyzed via primary and secondary processing data. The future enhancement of the Louisiana oyster industry hinges on improved production and value-added figures. As the state's coastal area diminishes, oyster producers will be implementing more forward-looking practices. These practices include private production of oyster seed and depuration. Public management agencies can also assist in the enhancement of Louisiana's oyster industry. To do so, however, the state must first recognize that spillover benefits to the public sector can result from oyster management leasing policy. To this extent, the oyster industry can help the state as the state aids the oyster industry.

KEY WORDS: oyster, Louisiana, economics

INTRODUCTION

The Louisiana oyster fishery is one of the state's older and more colorful commercial seafood industries. Dating back to at least the 1840's, the fishery has undergone a succession of changes, and indications are that more change is forthcoming.

Because of the dynamic nature of Louisiana's oyster fishery and its role at the national level, the overall goal of this paper is to provide an economic evaluation of the Louisiana oyster industry with reference to future prospects. To accomplish this goal, historical activities in the Louisiana oyster harvesting sector are first presented and are placed in context to regional and national activities. Since the Louisiana oyster industry extends beyond the dock and into wholesaling and processing, these activities and their linkage to the harvesting sector are presented in the second section. While the information presented in these sections focuses on past and current activities in the Louisiana oyster industry, it can be used as a basis for discussing future prospects. These prospects are evaluated in the final section.

HISTORICAL OYSTER LANDINGS

The oyster fishery is an important component of Louisiana's commercial fishing sector. With landings at dockside worth an estimated $31.0 million in 1987 (National Marine Fisheries Service, unpublished statistics), only shrimp ($184.2 million) and menhaden ($55.1 million) were more valuable than the oyster fishery.

Unlike the state's other marine fisheries, Louisiana's oyster harvest is largely derived from privately controlled, i.e., leased, grounds. Because of these leased grounds, which give their holders the incentive to maintain and improve on their assets and the state's expansive estuarine systems, Louisiana has established itself as the nation's largest oyster producer.

Louisiana Landings

The reported oyster harvest from Louisiana's waters for the 1961–87 period is given in Figure 1. As indicated, production has ranged from a low of 4.8 million pounds in 1966 to 14.3 million pounds in 1985, and has averaged 10.4 million pounds annually during the 27-year period. The vast majority of these landings have been concentrated in the eastern region of the state (see Figure 2), primarily in Plaquemines and St. Bernard parishes.

Though Louisiana's oyster production is relatively stable, there have been large deviations from the long-run average. These deviaitons generally reflect adverse environmental factors. The precipitous decline in the 1966 harvest, for instance, reflects the previous year's destruction of Louisiana's oyster reefs from Hurricane Betsy (United States Department of the Interior 1966). Similarly, the 1979–80 production decline can be traced to the opening of the Bonnet Carre Spillway near New Orleans which caused extensive damage to prime bedding areas in St. Bernard and Plaquemines parishes (Dugas 1985). Though production since 1982 has been well above the long-run average, much of this increase can be traced to increasing effort rather than favorable environmental conditions.

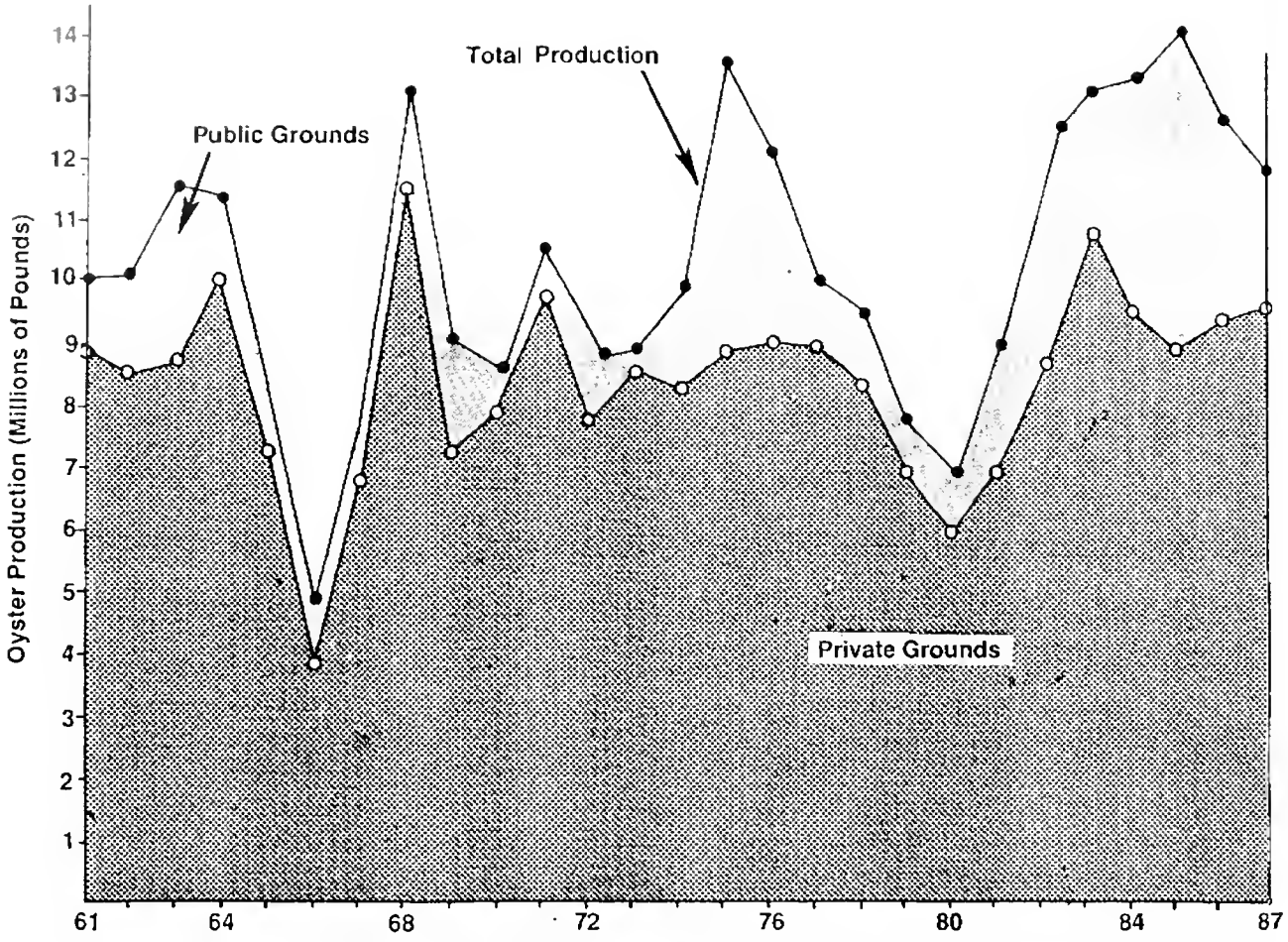

Figure 1. Louisiana private, public, total oyster production, 1961–1987.

The value of Louisiana's oyster production, though demonstrating variation in relation to annual yield, has been trending upwards (Figure 3). Averaging just less than $3.0 million annually during 1961–67, the value of Louisiana's reported oyster harvest increased to $6.8 million annually during 1971–77 and equalled $22.0 million annually during 1981–87.

Much of the increased value of the Louisiana oyster harvest is, of course, the result of inflation. Dividing the current value of Louisiana's oyster landings by the 1967 consumer price index removes inflationary effects and provides an estimate of value on a deflated basis. Expressed in this manner, the value of Louisiana's oyster harvest increased from an annual average of $3.2 million during 1961–67 to about $7.1 million during 1981–87, or about 120 percent. While this growth is impressive, it is considerably less than the more than 600 percent realized when value is examined on a undeflated, or current, basis.

The increase in the value of Louisiana's oyster harvest, expressed on either a current or deflated basis, has resulted from an increase in production and price. The increased production, especially since 1982, is illustrated in Figure 1. The increased dockside price is illustrated in Figure 4. While annual dockside price has increased during the 1961–87 period, it has fluctuated greatly. This fluctuation, according to Pawlyk and Roberts (1986), is largely in response to annual changes in Louisiana oyster landings. Their analysis which covered the 1961–81 period suggested that, at that time, a ten percent increase (decrease) in Louisiana's oyster landings will cause about a five percent decrease (increase) in the deflated dockside price. Oyster production outside Louisiana was found not to influence the Louisiana oyster dockside price structure. It is likely, however, that this situation has changed in the last couple of years. Because of a significant decline in U.S. and, especially, the Chesapeake production since 1981, as to be examined later, demand for Louisiana oysters has likely expanded in other regions of the country. As such, the decline in U.S. production in recent years is thought to have had a positive influence on Louisiana oyster prices.

Louisiana, as noted, depends heavily on privately controlled, i.e., leased, grounds for its annual oyster production. These grounds have historically yielded about 65–95% of total state oyster production (Figure 1). The

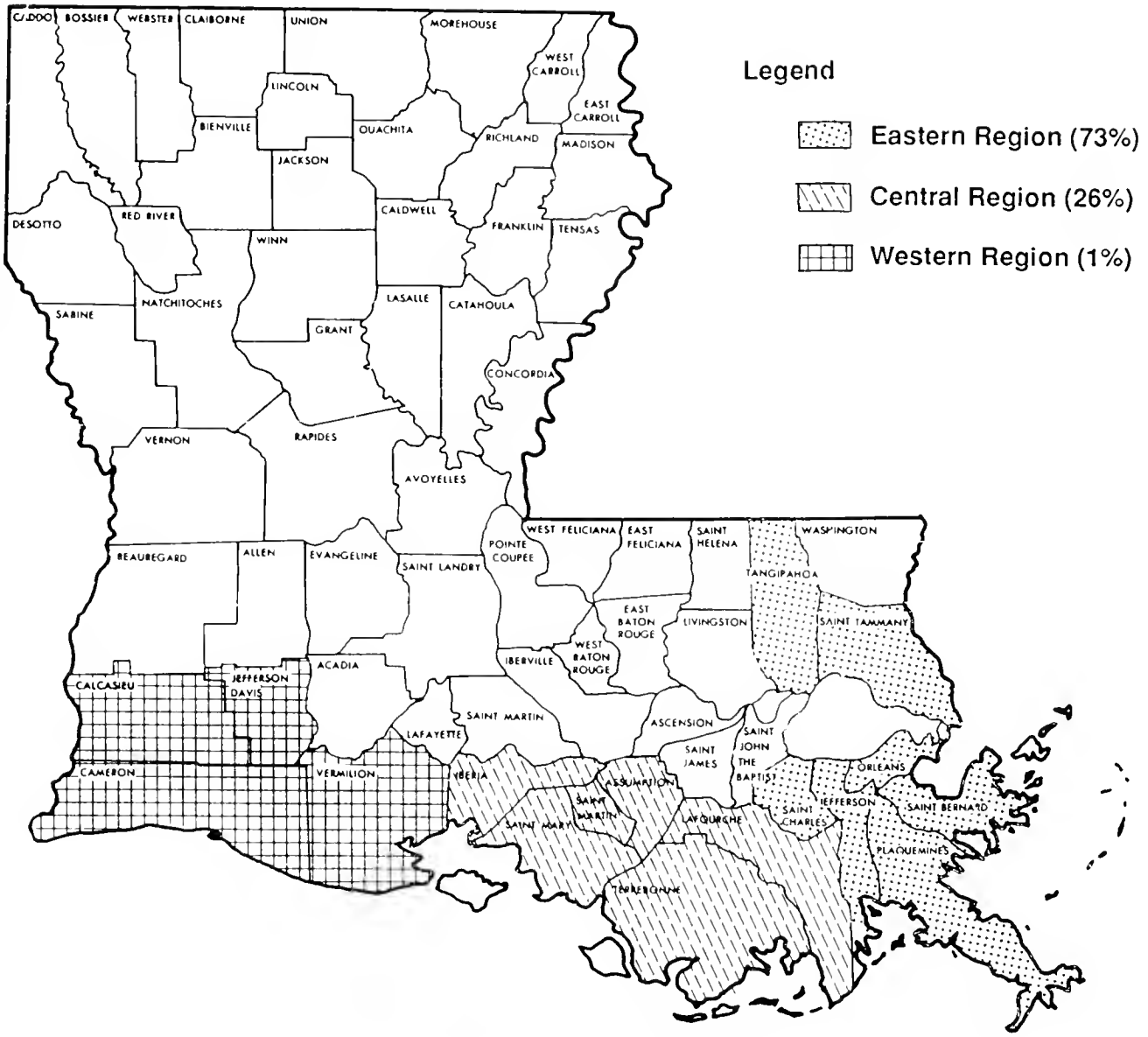

Figure 2. Regional distribution of Louisiana oyster landings, 1981–85.

public grounds, in addition to accounting for the remaining state production, provide an essential source of oyster seed. Each fall, as outlined by Chatry (1987), one- to three-inch oyster seed is taken from public oyster producing grounds, transported to leased grounds, and bedded. After six to nine months, these oysters reach marketable size and are harvested and sold. From two to three boat loads of marketable oysters are recovered for each boatload of oyster seed bedded (Chatry 1987).

An average of just over 80% of Louisiana's annual oyster harvest has traditionally been taken from private grounds. Because of the recent large increase in yield from public grounds (see Figure 1), the ratio of production from private grounds to total state production has fallen to an average of 74% since 1981. This increased yield from public grounds has contributed greatly to the recent overall increase in state oyster production. According to the Louisiana Department of Wildlife and Fisheries (Mr. Ron Dugas pers. comm.), this increased public grounds production has resulted from the opening of Calcasieu Lake to oystering and from the delayed benefits of the 1979 opening of the Bonnet Carre Spillway. The increased production from these activities, though a favorable sign for the oyster industry, is expected to be short-lived. In fact, 1986 and 1987 harvests have already declined (Figure 1), and the 1988 harvest is anticipated to be lower.

The oyster fishery, despite a relatively consistent yield throughout the 1960's and 1970's and an increased yield in the 1980's, is not as stable as the historical landings data would suggest. For example, though state oyster produc-

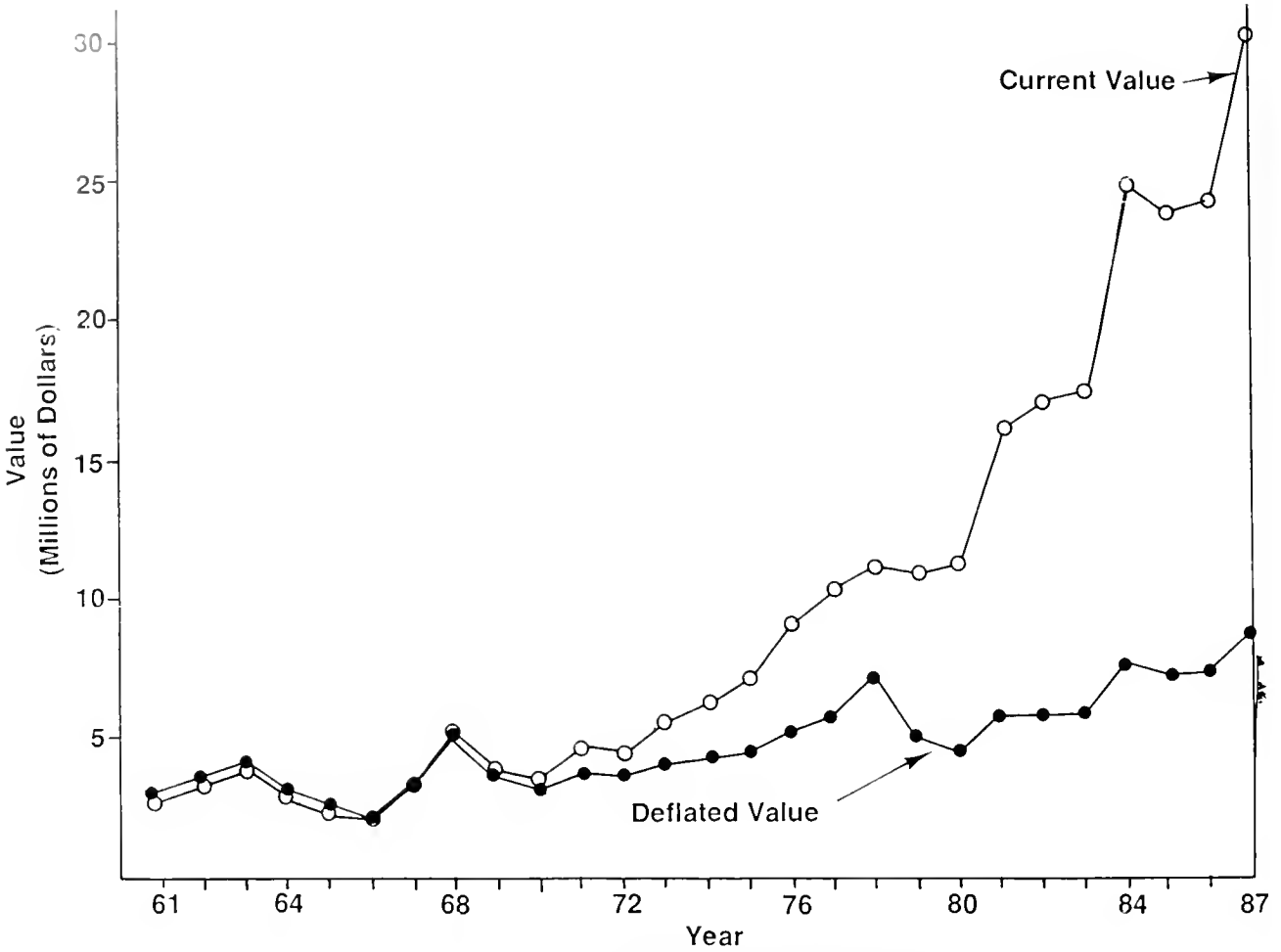

Figure 3. Current and deflated dockside values of Louisiana's oyster production, 1961–1987.

tion during the 1981–87 time period is about 20% above the long-range average, issuance of oyster dredging licenses by the Louisiana Department of Wildlife and Fisheries (code 144004) has increased well over one-hundred percent, from 390 in 1981 to more than 1,000 since 1985. The large increase in license sales during the 1980s indicates that catch per unit effort, i.e., dredge, has declined significantly in recent years. Also, though leased acreage has increased significantly, equalling 312 thousand acres in 1987–88 compared to 193 thousand in 1975–76 and 49 thousand in 1960, production from private grounds has shown very little growth. This indicates a declining production per acre of leased ground. While declining production per acre might be expected on the public grounds which are a common-property resource and thus subject to excessive effort, declining productivity on private grounds usually indicates more serious and long-term problems.

While some of the decline in oyster harvest per leased acre may be attributed to the recent increase in effort on public grounds, the deterioration of Louisiana's oyster beds is undoubtedly the reason for much of the per acre decline in productivity. This deterioration, the result of numerous factors, has been a slow but continuous process and has been well documented (see, for example, Van Sickle et al. 1976, Chatry et al. 1983). For example, saltwater intrusion along coastal Louisiana has destroyed many oyster beds and has left others vulnerable to predation by saltwater fish and shellfish species such as the black drum and oyster drill. Leveeing of the Mississippi River, while performing its primary function, control of water overflow, has left some oyster beds near the river and its tributaries void of the essential nutrients that were periodically deposited on these beds. With an increasing coastal population, pollution has resulted in permanent closure of many oyster beds and has resulted in others being opened only on a conditional basis. These and other factors have led to a decline in the size of the area producing seed oysters (Chatry et al. 1983) and a northward movement of producing oyster beds (Van Sickle et al. 1976). This northward movement and the encroaching levels of pollution southward (Van Sickle et al. 1976) could further jeopardize Louisiana's oyster industry.

Though measures have been taken to preserve Louisiana's remaining oyster grounds and create new suitable grounds, these measures have generally been very site spe-

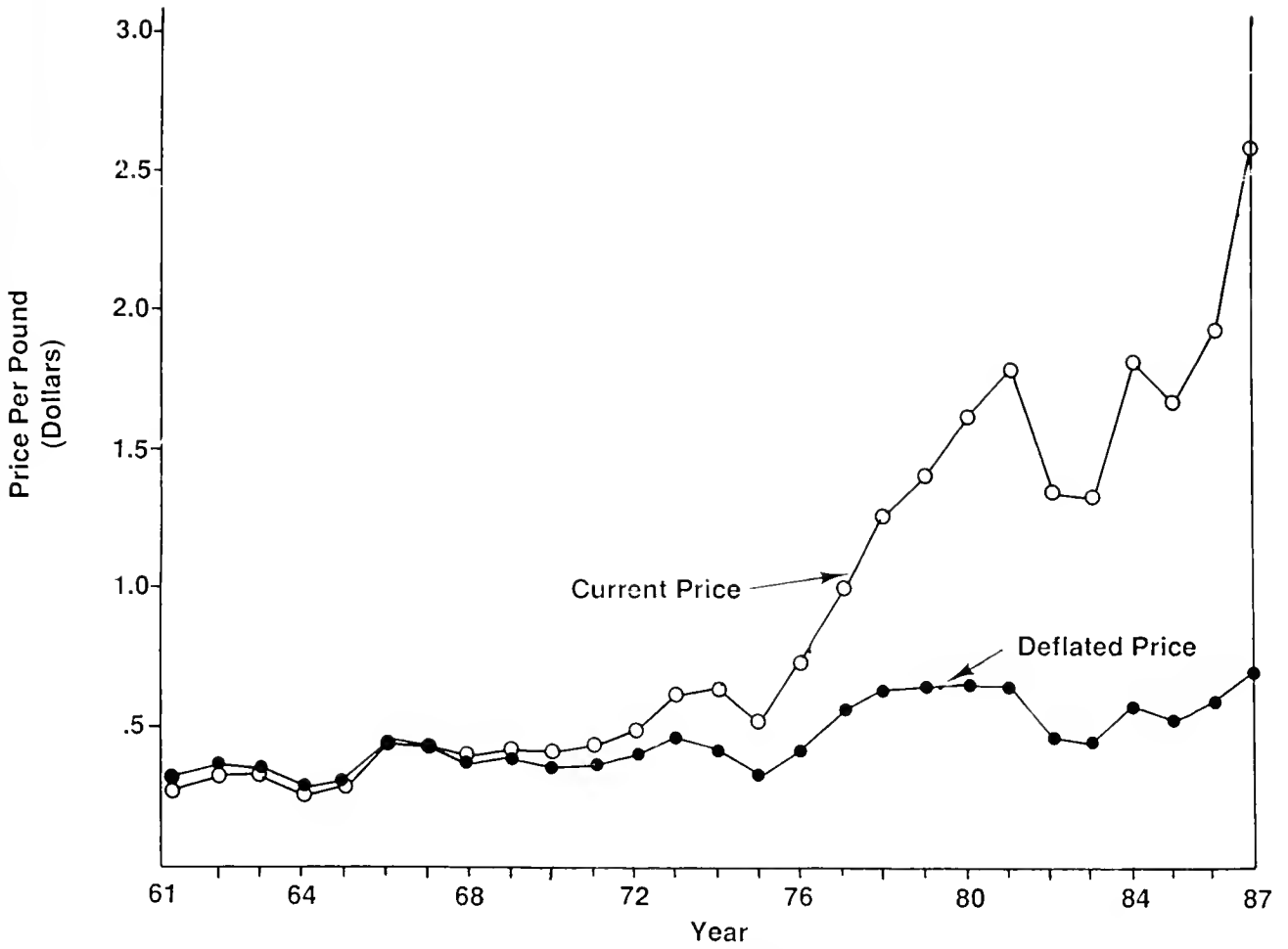

Figure 4. Current and deflated Louisiana dockside oyster prices, 1961–1987.

cific and conducted on a piece-meal basis. Because they have largely entailed construction of fresh-water diversion projects, they have been expensive and controversial (Dugas et al. 1981). Furthermore, it is generally recognized that until the state develops and implements a long-range plan suited to enhancement of the oyster industry, stop-gap measures of the type discussed above will provide the industry with only a temporary cure to its long-term problems.

Louisiana's Relative Production

Oysters are harvested in 18 of the 21 coastal states (Dressel et al. 1983). While the Eastern oyster (*Crassostrea virginica*) is primarily harvested along the East and Gulf Coasts of the United States, West Coast oyster production is dominated by the Pacific oyster (*Crassostrea gigas*). Annual Louisiana, East and Gulf Coast, and the West Coast oyster production for the 1961–87 period are given in Figure 5.

As evident from Figure 5, total U.S. oyster production has declined significantly since 1961 (this decline has actually been occurring since at least the early 1900's). Average annual production of 46.8 million pounds during 1981–87 is only about 80 percent of that reported during 1961–67. Production has fallen steadily and significantly since 1981 (Figure 5).

East and Gulf coast oyster production, with the exception of 1987, has represented 80–90 percent of the nation's total (Figure 5). Because of a large decline in the East and Gulf coasts' 1987 production in conjunction with an increase in West Coast production, the East and Gulf coasts' total declined to 75 percent.

Louisiana has historically been the largest oyster producer among Gulf states and second only to Maryland on a national basis. Because Maryland production has fallen sharply in recent years, Louisiana has recently established itself as the nation's largest domestic oyster supplier.

Though Louisiana's share of the nation's oyster production has fluctuated considerably during the 27-year period ending in 1987, it has generally represented 15 to 30 percent, with an average of 20 percent. Because of declining U.S. production and increasing Louisiana production during the 1980's, Louisiana's oyster production as a percentage of the U.S. total has been averaging about 30 per-

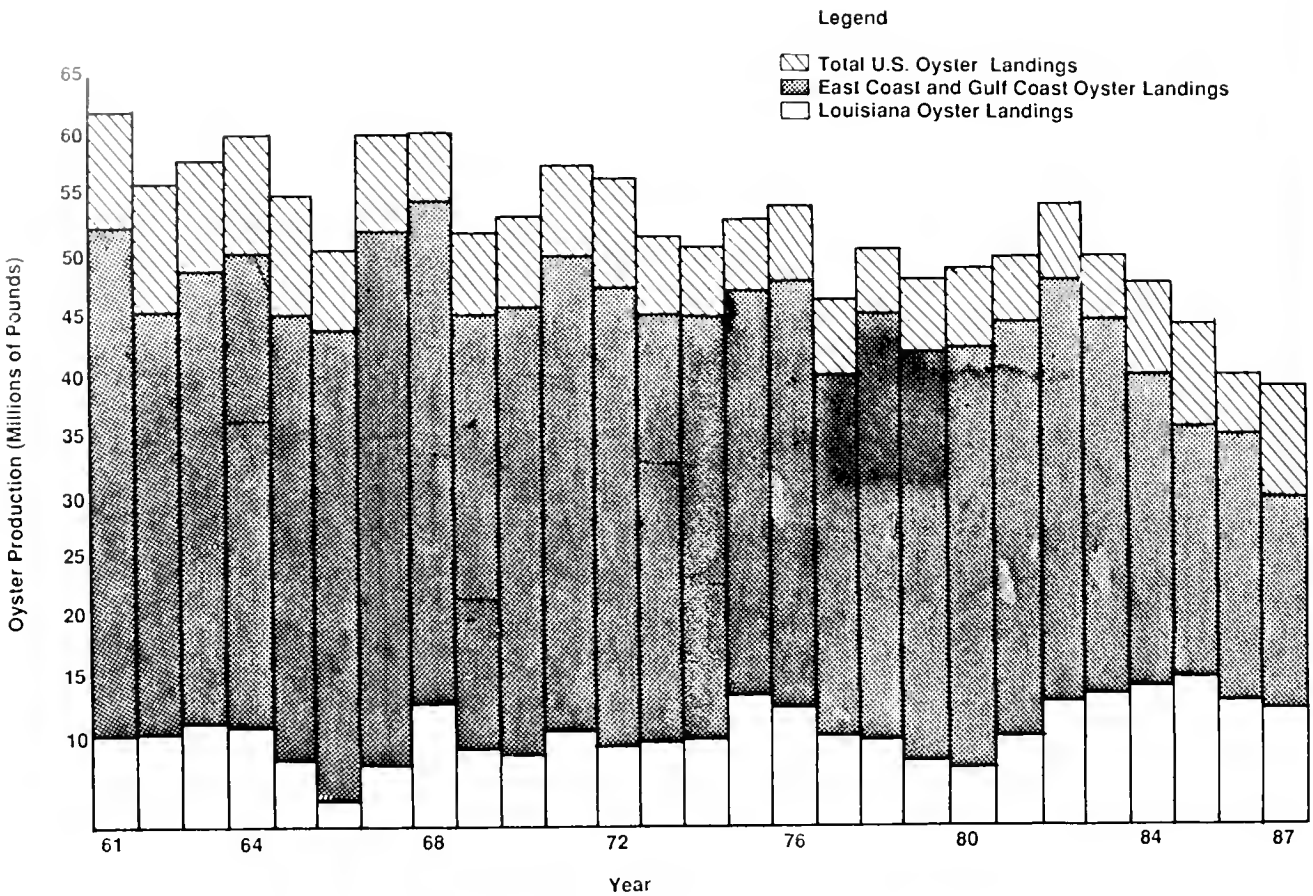

Figure 5. Louisiana, East Coast, Gulf Coast, and U.S. Oyster Landings, 1961–1987.

cent in recent years. With little indication of an increase in national oyster production in the near future, especially in the Chesapeake region where the oyster disease MSX, other diseases, and pollution (Haven et al. 1978) have devastated many of the major producing grounds, Louisiana will likely remain the major domestic oyster supplier.

Though U.S. oyster production has declined during the past several decades, the total oyster supply available for U.S. consumption has increased because of a large and growing oyster import market. These imports, which averaged just under 18 million pounds annually during the 1961–67 period and 24.6 million pounds during 1971–77, increased significantly to 38.3 million pounds during 1981–87. Imports of 52.1 million pounds in 1987 represented more than a three-fold increase over the quantity of oyster imports reported during the early 1960's.

These imports, largely from the Asian region, and especially from South Korea in recent years, generally enter the United States as a canned product. Since little of the U.S. oyster harvest is currently canned, the current degree of competition between imported oyster products and domestic harvest is debatable. It is generally believed, however, that the canned import market has displaced the U.S. oyster canning industry which was once quite large in some states such as Louisiana.

WHOLESALING AND PROCESSING ACTIVITIES

Wholesaling and processing activities, though representing important components of the U.S. fishing industry structure, are often overlooked in the setting of management policy. Since these components can provide additional employment and revenues, omission of them in management formation may result in suboptimal policy, especially when employment or revenues enter the management objective function. Also, to the extent that many fisheries are producing at or near their maximum, future revenue increases will require improved wholesaling, processing, and marketing techniques. The Louisiana oyster industry, in lieu of significant change in management and enhancement techniques, may be a good case in point. Current and historical wholesaling and processing activities for the state and in relation to the Gulf region are examined below. This examination will help analyze future prospects in this area.

Current Activities

The National Marine Fisheries Service Statistical Division lists 63 primary dealers, i.e., first buyers, of Louisiana oysters in 1985 (Mr. Ernie Snell pers. comm.). About 40 percent of the 14.3 million pound 1985 harvest was handled by the largest four of these primary dealers. The largest 10

dealers handled more than 60 percent of the total 1985 state harvest. Fifty percent of these dealers handled about 95 percent of production.

Twenty-seven of these primary dealers and an additional three processors not on the list of first dealers were interviewed in the fall of 1986. These interviews were made for the purpose of documenting procurement and marketing activities in the Louisiana oyster industry during the 1985–86 oyster season, i.e., September 1985 through August 1986. This analysis, though representing only the thirty dealers, is thought to be indicative of practices within the Louisiana oyster industry.

An overview of initial oyster procurement among the 30 interviewed companies is provided in Figure 6. Altogether, these 30 dealers reported purchasing or taking 1.2 million sacks of oysters (7.2 million pounds of oyster meat based on six pounds of meat to the sack) from independent fishermen or their leases. Two-thirds of these 1.2 million sacks were harvested from private grounds while the other third came from public grounds. The thirty interviewed dealers/processors also secured another 247 thousand sacks of oysters from out of state, primarily Texas. Another 233 thousand sacks were purchased directly from other Louisiana oyster dealers and thus represent transshipments. Combining these three sources of supply (i.e., direct purchases from fishermen and oysters taken from leases, out-of-state procurement, and transshipments), interviewed Louisiana dealers had 1.7 million sacks of oysters for processing and/or sale.

Processing and marketing activities related to the 1.7 million sacks of oysters handled by the 30 interviewed dealers are illustrated in Figure 7. The majority, about 60 percent of the total, was resold as sacked oysters (some of this amount may represent the transshipments discussed above). A small amount, about 7 percent of the total, was boxed. The final third were shucked and marketed in various sized containers. No further processing activities, such as breading, were conducted among interviewed dealers.

Thirty-five percent of the sacked and boxed oyster trade was directed to in-state markets (Figure 7) while the other 65% was directed to out-of-state markets. The vast majority of these out-of-state shipments was sacked oysters which were primarily destined for processing lines in Alabama, Mississippi, and the Florida Panhandle. Survey results indicated that an estimated 30–35% of Louisiana's 1985–86 oyster harvest was, in fact, processed out-of-state. In addition, some of the sacked oyster originally sold in the state may eventually have been resold to out-of-state processors who may have utilized these purchases in their processing lines.

Of the shucked product, 58% was directed toward out-of-state markets while 42% was sold in state. An unknown amount of these in-state sales may eventually have left the

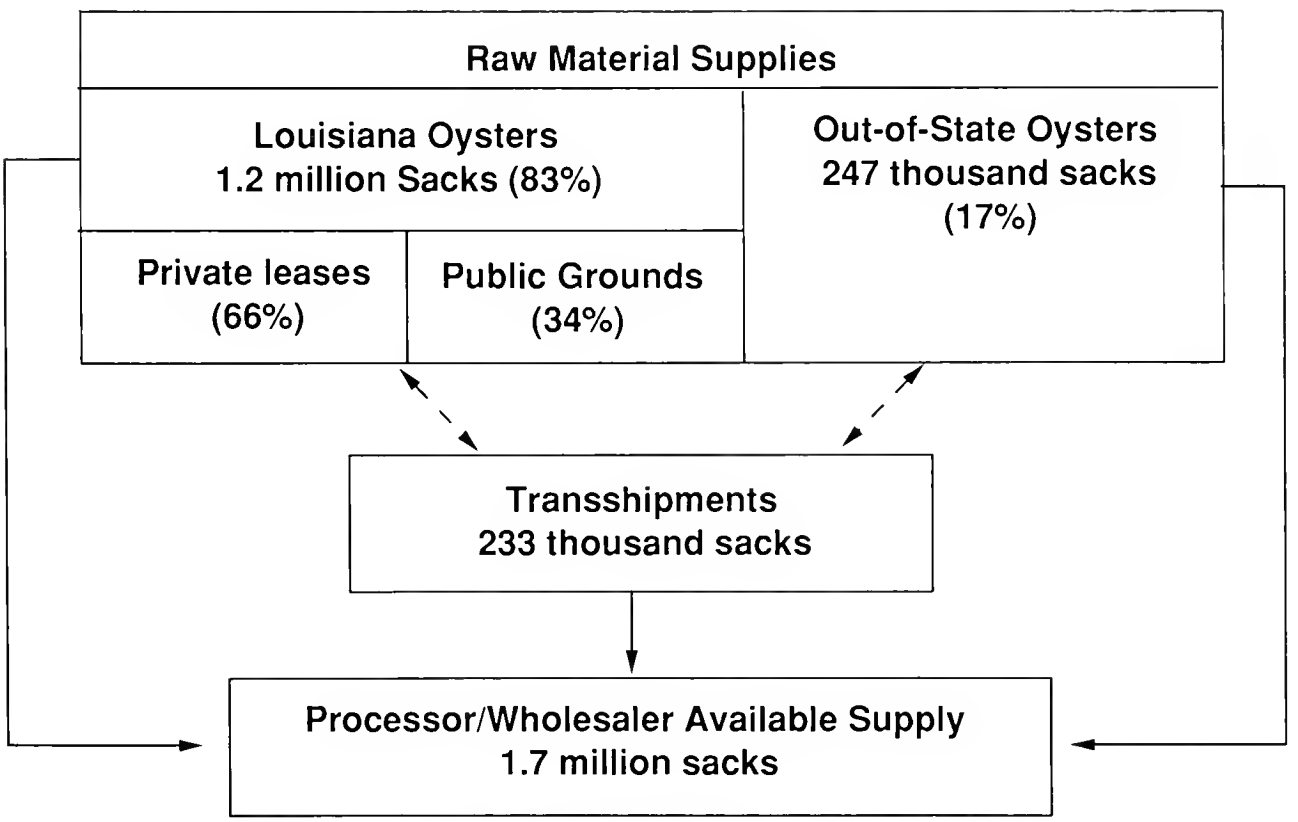

Figure 6. Sources of wholesaling and processing oyster supply (in sacks of oysters, 1985–86).

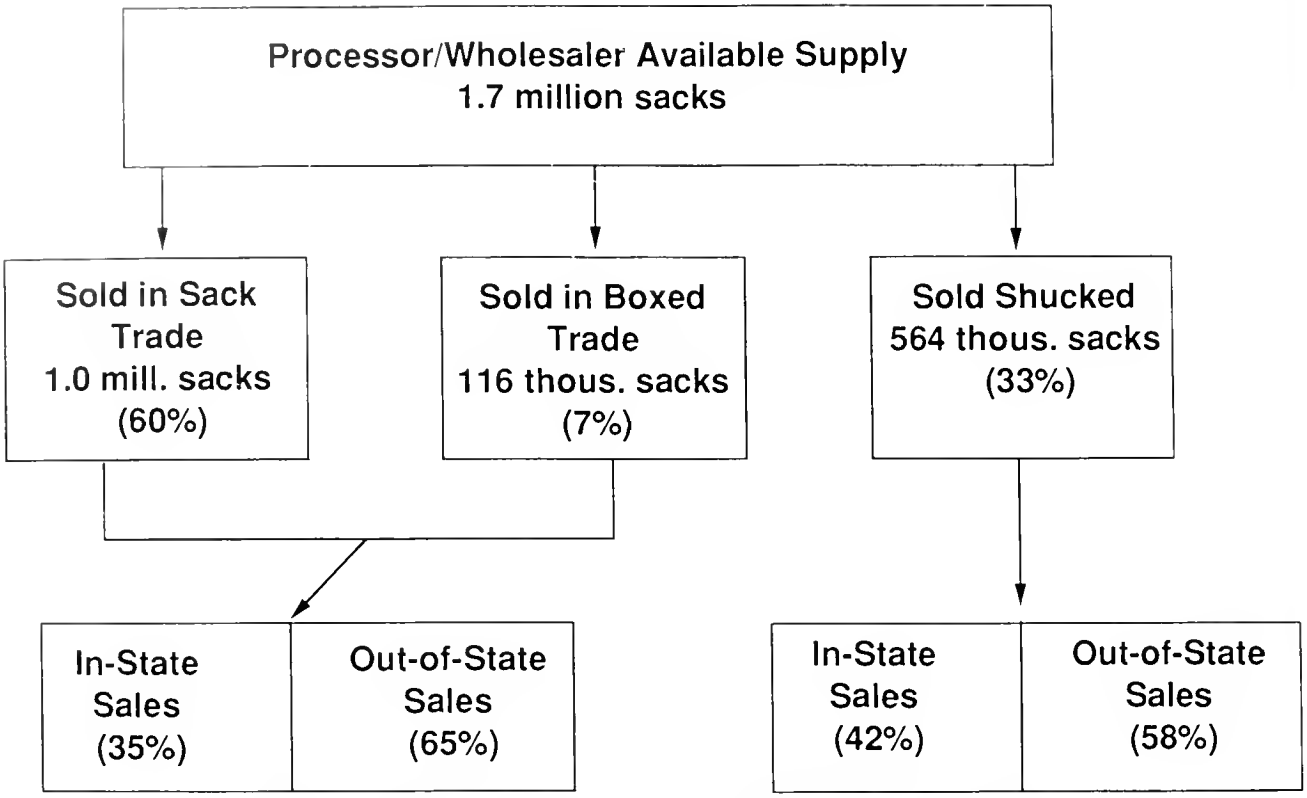

Figure 7. Product form distribution used by Louisiana wholesalers/processors, 1985–86.

state as it was moved through secondary outlets. Though not examined in this study, some of the out-of-state shipments of shucked oysters may have been subject to additional value-added services, such as breading.

Historical Processing Activity

Louisiana, as a rule of thumb, accounts for about one-half of the annual Gulf region oyster harvest by poundage. For instance, Louisiana's oyster harvest represented 50% of the Gulf region total during the 1981–85 period compared to 51% during 1976–80 and 59% during 1971–75. Oyster processing activities in the state, however, are generally well below 50% of the Gulf region total and appear to be declining (Table 1).

While accounting for 59 percent of the Gulf region harvest during 1971–75, Louisiana accounted for only 38.5%

TABLE 1.

Louisiana and Gulf Regions Processed Oyster Value, 1971–86.

Time Period	Value of Processed Oyster Products		Louisiana as % of Gulf
	Louisiana	Gulf Region	
	Million Dollars		
1971–75 avg.	9,338	24,272[a]	38.5
	(6,796)[b]	(19,848)	
1976–80 avg.	11,997	37,621	31.9
	(6,067)	(19,119)	
1981–85 avg.	16,024	56,797	28.2
	(5,350)	(18,963)	
1986	17,264	57,434	30.0
	(5,257)	(17,489)	

Source: Unpublished data provided by the National Marine Fisheries Service, Fisheries Statistics Division.

[a] The estimates of Gulf region processed oyster value provided here exceed those given in *Processed Fishery Products, Annual Summary*. This is because values given in this table include unclassified processed oyster products.

[b] Numbers in parentheses refer to the deflated value (i.e., corrected for inflation) of oyster processed products with 1967 equalling the base year.

of the value of oyster processing activities (Table 1). Similarly, though Louisiana's share of the Gulf region oyster harvest equalled 51% during 1976–80, its share of Gulf region oyster processing activities equalled only 32% by value during that period and only 28% by value during the 1981–85 period. Furthermore, though the deflated value of Louisiana's annual oyster harvest has increased significantly since the early 1970's (see Figure 3), the state's oyster processing activities have declined sharply.

Several explanations can be given for Louisiana's relatively small and declining share of Gulf region oyster processing activities. First, as previously discussed, much of Louisiana's oyster harvest leaves the state in sack to be processed in Alabama, Mississippi, and the panhandle of Florida (see Prochaska and Keithly 1985, for a discussion of the use of Louisiana oysters among Florida-based processors). Second, though Louisiana oyster companies do conduct primary processing activities, i.e., the shucking of oysters, they perform very little additional value-added services, such as the breading of oysters. These services are conducted in other Gulf States, especially Florida. A final explanation for Louisiana's relatively small and declining share of Gulf region oyster processing activities reflects the demise in the Louisiana oyster canning business. This business, once an important segment of Louisiana's oyster industry, had disappeared by the early 1980's (Dugas et al. 1981), largely the result of import competition in the form of canned oysters originating from South Korea and Japan.

Though Louisiana does less oyster processing than might be expected given its relative landings, per establishment sales of processed oyster by Louisiana oyster processing establishments exceed the Gulf region average (Table 2). However, because less than a fourth of the Gulf region oyster processing establishments are generally Louisiana-based (Table 2), total oyster processing activities in Louisiana in relation to the Gulf region are less than that state's share of landings.

Though Louisiana does have oyster processing establishments larger than the Gulf region average, their processing activities have been declining when examined on a deflated basis. Compared to a 1971–75 average of $161 thousand, processed oyster sales per Louisiana oyster processing establishment fell to $116 thousand during the 1981–85 period. On a Gulf-wide basis, however, deflated processing revenues have remained relatively constant. The decline in establishment processing activities in Louisiana may reflect the demise in the oyster canning industry and increased out-of-state competition for Louisiana's oysters.

FUTURE CONSIDERATIONS

The future impact of the Louisiana oyster harvesting sector hinges on public investments and private actions. The former are exemplified by the U.S. Army Corps of Engineers' proposed freshwater diversion projects. With respect to the latter, lessees are currently evaluating procedures involving more efficient use of cultch, depuration, and additional processing.

Physical loss of marsh, subtle encroachment of high salinity water, and poor quality water necessitate success in public and private endeavors. Production in the 12 to 14 million pound range since 1982, accounting for up to 30 percent of United States landings, may deflect interest of the public sector. Such prevailing thought, however, is short-sighted, since Klima (1988) has proposed explanations for the recent favorable landings of estuarine-dependent species. His investigations indicate estuarine areas in physical decline may enhance production up to some inevitable point signifying a major prolonged decline. The prospect of this scenario puts the public and private investments in the realm of necessity.

TABLE 2.

Louisiana and Gulf Region Oyster Processing Establishments and Processed Oyster Sales Per Establishment, 1971–86.

Time Period	Louisiana		Gulf Region	
	Number of Establishments	Oyster Sales per Estab.	Number of Establishments	Oyster Sales per Estab.
		($1,000)		($1,000)
1971–75 avg.	42	221.3	183	132.8
		(161.0)[a]		(96.4)
1975–80 avg.	39	304.5	187	201.2
		(154.0)		(99.4)
1981–85 avg.	45	352.9	196	290.1
		(116.3)		(97.4)
1986	43	401.5	159[b]	361.2
		(122.6)		(110.0)

Source: Compiled from unpublished data provided by the National Marine Fisheries Service, Fisheries Statistics Division.

[a] Numbers in parentheses refer to the deflated value (i.e., corrected for inflation) of oyster processed products with 1967 equalling the base year.

[b] The decline in 1986 Gulf region oyster processing establishments in relation to the previous five-year period reflects the destruction of Florida-based establishments in 1985 by Hurricane Eleana.

Corps-directed freshwater diversion plans are a mix of near-term prospects and more distant projects. As of this writing, the diversion of some Mississippi River flow into the Breton Sound Basin is under construction and diversion projects into the Barataria and Pontchartrain Basins are pending. Feasibility analyses performed for the Pontchartrain Basin project, for example, identify an impacted area which includes a large portion of the state's public reefs and leased acreage. These analyses identify the projects value in terms of the declining resource base and revitalizing the industry. Louisiana's additional landings to be derived from this project, primarily from dredge gear (98%), are projected to approximate 2 million pounds. Efficiency should be improved at the higher harvest as reflected by the forecasted 60 percent reduction in aggregate harvest cost. The pace of project implementation and increased production may have little market impact. The Corps analyses cite the long-term decline in Chesapeake Bay production.

Efforts by lessees to stabilize and improve production may include heretofore unconventional procedures for Louisiana. More effective management of cultch via use of bagged shells to catch spat is an example of a yield-increasing strategy. The procedure uses 250 washed oyster shells per one-half inch mesh bag. Sixteen bags are placed on pallets in four layers of four bags. Placement on a lease occurs when monitored salinity, water temperature, plankton, and larval levels indicate suitable conditions. The purpose is to catch and grow spat to one-quarter inch size. Bags are to be broken onto hard reefs when cooler water temperatures signal lessened predation risks. This costly process in terms of labor and materials is being evaluated as one possible means of increasing yield. The feasibility for many lessees to follow this procedure is unknown.

Larger investments are also possible as a means of marketing more oysters from leases. Many areas produce oysters which are not marketable due to the conditional classification of the water. Use of ultraviolet and ozone systems to cleanse oysters of indicator bacteria is a procedure being tested by at least two Louisiana companies. While this procedure is widely used in Europe, its potential remains undeveloped in Louisiana. Concern exists over the capability and reliability of depuration to cleanse oysters of viruses within the time limits established for the indicator bacteria.

Even in the absence of depuration, there appears to be room for expansion in the Louisiana oyster processing sector. The state, because of a declining oil-based economy, has begun to recognize the importance of its seafood processing sector and encourage its further development. Actions taken by the state for development purposes include creation of the Louisiana Seafood Promotion and Marketing Board and providing economic incentives. Expansion of the processing sector will certainly generate increased oyster industry revenues through time and stimulate additional employment in the industry.

In conclusion, it does appear that procedures to further enhance Louisiana's oyster industry will necessitate public sector projects and the economic incentives to motivate lessees. Given that 80 percent of landings originate from leases, it is perhaps inevitable, and necessary, for broader-based public effort to stimulate private production. There may be incentives in model leasing regulations tailored to specific high erosion areas which need evaluation. Adoption of a viewpoint that oyster ground lessees can undertake actions which provide public benefits is necessary. It is particularly important in Louisiana because the oyster industry is increasingly being viewed at this time in terms of balancing the management agency budget. Severance taxes, license revenue and rental fees from leases are being compared to agency expenditures for oyster management. The actions of lessees to build and stabilize hard bottoms in dynamic estuarine areas have benefits beyond those received by the producer. Recognition of these spillover benefits to the public sector should stimulate management agencies to adopt policies enhancing reef building activities. In the absence of sensitivity to this matter, management agencies could implement policies of perceived value to the agency but detrimental to the industry's and state's long run interests.

ACKNOWLEDGMENTS

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SHELLFISH SANITATION STUDIES IN LOUISIANA

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ABSTRACT Shellfish sanitation is based on allowable numbers of fecal coliform "indicator" bacteria in shellfish and growing waters. However studies of the relationships between enteric viruses and bacterial indices in Louisiana oysters and waters indicated that viruses do not always correlate with the fecal coliform indicator system. This system was further questioned when Louisiana oysters harvested from approved growing waters in summer months contained high levels of non *E. coli* fecal coliforms which were not of sewage origin. This problem resulted in an interim *E. coli* rather than fecal coliform guideline in oyster meats. However the standard 10 day method for the enumeration of *E. coli* in shellfish was not feasible for perishable shellstock oysters. A study of several rapid methods for *E. coli* in Louisiana oysters proved that a 48 hour fluorogenic methyl umbelliferone glucuronide (MUG) assay was very sensitive for *E. coli* in oysters with high fecal coliform to *E. coli* ratios. The concern with non-sewage related marine *Vibrio* pathogens in Louisiana oysters resulted in studies using ionizing radiation to eliminate *Vibrio* spp. from shellstock oysters. Levels of 1.0 KGy (100,000 rads) of gamma irradiation reduced all *Vibrio* pathogens to undetectable levels, but were not lethal to shellstock oysters. Sensory evaluation of radiation processed raw oysters showed no significant difference from the non-irradiated controls.

KEY WORDS: shellfish sanitation, indicators, rapid methods, irradiation processing

INTRODUCTION

Louisiana ranks first in the nation in oyster production. In 1987, landings totaled about 12 million pounds with an ex-vessel value of approximately $30 million (NOAA 1988). When this is extrapolated to the retail sales level, the value of the industry can increase many times. The additional economic impact of jobs in the coastal areas and industry related businesses makes the oyster industry very significant to the overall economy of the state (Dugas et al. 1983). However, productive oyster growing estuaries are diminishing at an alarming rate. The intrusion of salt water from the sea brings predators and parasites that push the productive zone inland, and the encroaching sewage pollution from coastal runoff pushes the approved growing zone seaward. Approximately one half of the productive growing waters in Louisiana may be closed for shellfish harvesting at certain times of the year (Broutman and Leonard 1988).

Domestic raw sewage contains extremely high numbers of the fecal coliform bacterium *Escherichia coli*. The standard method for the indication of this type of pollution in growing waters and shellfish is the determination of most probable numbers (MPN) of fecal coliforms (APHA 1976; AOAC 1984, APHA 1985). These are considered to be "indicators" of the possible presence of more serious enteric bacterial pathogens (e.g. *Salmonella* spp.), and the enteric viruses (e.g., Hepatitis type A and Norwalk virus). Shellstock and processed raw oysters must meet the wholesale market criteria of total aerobic plate counts of 500,000 or fewer microorganisms per gram of oyster meat, and oyster meat guidelines of 230 MPN fecal coliforms/100 grams. The safety evaluation of these oysters is based on an allowable standard of 14 MPN fecal coliforms/100 ml in growing waters (APHA 1976, APHA 1985, USFDA 1988).

STUDIES OF ENTEROVIRUSES AND BACTERIAL INDICATORS AND PATHOGENS IN LOUISIANA OYSTERS AND OVERLYING WATER

In the fall of 1982, approximately 500 cases of viral gastroenteritis associated with the consumption of raw oysters taken from approved growing waters were reported to the Louisiana Department of Health and Human Resources. Retrospective sampling of the suspect growing waters showed levels of fecal coliform indicator bacteria in the overlying waters were in excess of the allowable 14 MPN fecal coliform/100 ml standard. Enteric viruses were also recovered from these waters. However, studies in the last decade have indicated that standard fecal coliform bacterial indicators do not necessarily correlate with the presence of human enteric viruses in shellfish and growing waters (Gerba and Goyal 1978, Ellender et al. 1980, Cole et al. 1986B).

A year of field studies was conducted to determine if there was any correlation between viruses, bacterial indicators (fecal coliforms) and bacterial pathogens (*Salmonella* and *Vibrio parahaemolyticus*) in Louisiana oysters and overlying waters. Approved and closed growing areas were sampled monthly. Samples of 20 to 30 oysters were collected with a small dredge. Overlying water samples of 380

liters were collected simultaneously for enteric virus recovery with a simplified large volume virus concentrator developed for brackish (5 to 25 ppt) oyster-growing waters. No significant differences in virus recovery were found at salinities of 7, 14, or 20 ppt. There was some decrease at 25 ppt, but oyster propagation is optimal at 14 to 20 ppt (Cole et al. 1986b). Overlying water samples and oyster meats were analyzed for bacterial pathogens and fecal coliforms by APHA approved methods (APHA 1985). Several methods for the recovery of enteric viruses from Louisiana oysters were compared to determine the most efficient and feasible procedure for routine field studies in Gulf Coast oysters. The methods were compared for ease of extraction, cytotoxicity, bacterial contamination and most importantly, recovery rates and final volume. A modified method of Ellender et al. (1980) was chosen to use in the field studies (Cole et al. 1986a).

The results of this study showed an inverse relationship between the presence of virus in water and temperature, salinity, conductivity and pH. There was no statistical correlation between levels of viruses in overlying waters and in oyster meats. There was no statistical correlation between *V. parahaemolyticus* and fecal coliforms or enteric viruses. No *Salmonella* were detected in oysters or overlying waters. Overall, statistical analyses showed no correlation between presence of enteric viruses and fecal coliforms in growing waters or oyster meats. These results question the validity or reliability of a fecal coliform indicator for enteric virus in shellfish and growing waters.

SEASONAL VARIATION IN THE FECAL COLIFORM POPULATION IN LOUISIANA OYSTERS

In the summer of 1982, Louisiana oysters harvested from "approved" growing waters were embargoed in East Coast receiving states because of excessively high counts of fecal coliform "indicator" bacteria in the oyster meats. The resulting economic losses to the Lousiana industry and to the East Coast receiving states were significant.

An extensive study was conducted on the nature of the fecal coliform population of Louisiana oysters and the growth of these organisms during interstate shipment (Paille et al. 1987). Oyster, water and sediment samples from open and closed growing areas were taken every month for one year. The fecal coliform population was analyzed by APHA approved methods (APHA 1985). Further biochemical characterization of the fecal coliform positive isolates showed that *E. coli* was the predominate fecal coliform when the water temperature was below 21°C. However, non-*E. coli* fecal coliforms predomianted during warm weather (May through September). *Klebsiella pneumonia* isolates accounted for 86% of the non-*E. coli* fecal coliforms, and often outnumberred *E. coli* 1000 to 1. These oyster isolates were further characterized and compared with *K. penumonia* clinical isolates by electron microscopy, guanine:cytosine ratios and antibiotic resistance. The results of these studies suggested that the fecal coliform positive *K. pneumonia* strains isolated from oysters were of environmental and not sewage origin. Their seasonal variation was typical of enviromental bacteria, and they did not exibit the multiple antibiotic resistance characteristic of the clinical strains. Similar studies by the U.S. Food and Drug Administration concurred that Gulf Coast oysters harvested from approved growing waters in summer months may contain excessively high levels of non-*E. coli* fecal coliforms and not represent a health hazard (GCTSU, USFDA 1983).

It was concluded that fecal coliforms may not be a reliable indicator of fecal contamination in Gulf Coast oysters in summer months, and that *E. coli* would be a better indicator for an oyster meat guideline. This resulted in the adoption of an interim oyster meat guideline of 230 MPN *E. coli*/100 g instead of 230 MPN fecal coliforms/100 g by the Interstate Shellfish Sanitation Conference (ISSC) in 1983. However, the APHA approved method for the enumeration of *E. coli* in shellfish takes 10 days to complete. This is not economically feasible for routine inspections of perishable shellstock oysters in state health laboratories.

This initiated studies for the more rapid enumeration of *E. coli* in oysters.

RAPID METHODS FOR THE ENUMERATION OF *E. COLI* IN OYSTERS

Several rapid methods for the enumeration of *E. coli* in oysters were evaluated and compared with the standard 10 day APHA method (Kilgen et al. 1985). These included an 8 day Modified A-1 method of Hunt and Springer (1978); a three day modified A-1 method suggested by an Ad Hoc Microbiology Committee of the 1983 ISSC (the IMViC series of biochemical tests for the confirmation of *E. coli* was shortened from 5 days to 24 hours by using the indol and citrate tests only); a 24 hour Anderson Baird-Parker assay (1975), and a 48 hour fluorogenic assay of Feng and Hartman (1982) using lauryl sulfate tryptose (LST) and EC-MUG (methylumbelliferone glucuronide). This is a fluorogenic assay for the enzyme beta-D-glucuronidase (GUD) produced by 97% of *E. coli* strains (Hartman et al. 1986). The fluorogenic compound was originally incorporated into the primary LST medium, but the GUD enzyme was also produced by the oyster tissue.

Results of this study showed no statistically significant differences in recovery of *E. coli* between the APHA method and A-1 methods or the EC-MUG method. The Anderson Baird-Parker method was not suitable for oyster meats with high fecal coliform to *E. coli* ratios. Dilutions of oyster meats high enough to have countable colonies did not recover *E. coli*. The EC-MUG method was the most rapid and efficient, and was actually more sensitive to enumerate *E. coli* in oyster meats with high fecal coliform to *E. coli* ratio.

The concern with non-sewage related marine *Vibrio*

pathogens in shellfish has increased in the last few years. *Vibrio* species are naturally occurring marine organisms which are found in the greatest abundance in very warm waters with high salinities (Colwell 1984). *Vibrio parahaemolyticus, V. cholerae* and *V. vulnificus* are three of the species of health risk concern. *Vibrio vulnificus* causes the greatest concern because it can cause high mortality septicemias (>50%) in high risk individuals. These are persons with such health problems such as chronic liver disease, diabetes and immunosuppression. Education and research efforts to solve this problem have been urged by federal and state health regulatory officials (Tuttle 1985, Food Chemical News 1988).

These concerns with marine *Vibrio* pathogens resulted in a study to evaluate gamma irradiation processing of shellstock and shucked Gulf Coast oysters to eliminate these organisms.

CONTROL OF INDICATOR AND PATHOGENIC BACTERIA IN GULF COST OYSTERS BY IONIZING IRRADIATION

Ionizing irradiation has been investigated extensively in the past as a potential preservative for fresh seafoods (Josephson and Peterson 1983). The lethal $dose_{50}$ of ionizing irradiation in live shellstock oysters was determined 24 hours after treatment with dose levels of 0.5 to 3.0 Kilo-Gray (KGy). Viability was determined by presence of "gaping valves," ciliary action and heartbeat. The LD_{50} was 2.25 KG (225,000 rads). Live oysters were then seeded by feeding them with high levels (10^4 to 10^6 MPN/g) of indicators (*E. coli*, and a fecal coliform positive *Klebsiella pneumonia* environmental oyster isolate), and pathogens of public health significance (*Salmonella typhimurium, Vibrio cholerae* and *Vibrio parahaemolyticus*). The seeded oysters were then processed with sublethal doses of ionizing irradiation (0.5 to 1.5 KGy) to evaluate its effectiveness in eliminating or significantly reducing the seeded bacterial pathogens and indicators. Some of the seeded oysters were shucked aseptically before irradiation processing to evaluate any absorbing effect of the shell. Fresh shellstock oysters were also processed at a sublethal dose of 1.5 KGy for sensory evaluation with control non-irradiated oysters from the same sack.

Results showed that all *Vibrio* species were reduced to undetectable levels at 1.0 KGy. *E. coli* dropped to undetectable levels at 1.5 KGy. *Klebsiella* and *Salmonella* showed 2 log reductions at 1.5 KGy. Total aerobic plate counts were also reduced 2 logs at 1.5 KGy. There was no significant difference in the effect of radiation processing on shellstock or shucked oysters. Sensory evaluation showed no significant organoleptic differences in shellstock oysters processed at the sublethal dose of 1.5 KGy (Kilgen et al. 1987).

CONCLUSIONS

Our coastal estuaries are the most productive waters in the world. Abundant shellfish populations have always fluorished in these waters. They have been an important source of food and are of vital importance to the economy of many states. However, problems with the current system of sanitary classification of shellfish growing waters based on the fecal coliform indicator standard, and alarming publicity reports concerning the possible presence of *Vibrio* marine pathogens in shellfish have caused a significant lack of confidence in the system by industry members, regulatory officials, university researchers and, most importantly, the consumer public. Results of these studies have addressed some of these problems and concerns. However, there is a need to develop and support further research in these areas. Depuration as a method to eliminate sewage-related and marine *Vibrio* pathogens in shellfish is a more consumer acceptable method than ionizing irradiation. Collaborative studies of the effectiveness and economic feasibility of a commercial oyster depuration facility in Louisiana are currently being developed.

The need for a national collaborative study to re-evaluate the sewage pollution indicator system used for growing water classification has been advised for many years by all groups concerned. A current collaborative effort is a four year study at the national level consisting of university, industry and shellfish regulatory members. This study will evaluate the relationships among indicator criteria, human enteric pathogens and potential health risks in a total environmental assessment of representative shellfish estuaries throughout the country.

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AN OYSTER FARMER'S PERSPECTIVE TO THE PAST, THE PRESENT, AND THE FUTURE OF THE LOUISIANA OYSTER INDUSTRY

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ABSTRACT The Louisiana oyster industry has a long history dating back to the mid 1800's, and, as the annual production figures will indicate it has its ups and downs. Present production ranks it first nationally; however, overall production is being constrained by environmental degredation, and per capita harvests are down due to the increasing number of fishermen as a result of the declining Louisiana oil economy, and other factors. There will have to be changes made to the way the industry does business and the way the "Public Seed Grounds" are managed to make segments of this industry economically solvent.

KEY WORDS: Management, oysters, Louisiana, industry

INTRODUCTION

The Louisiana oyster industry has always been of economic importance to the State of Louisiana. Besides contributing to the national consumption of oysters, the industry also contributes to the rich culture and heritage of Louisiana.

Oyster (*Crassostrea virginica*) production in Louisiana over the past several years has averaged nearly 12.5 million pounds annually with a dockside value of approximately 23 million dollars. The 1985 landings of 14.2 million pounds was valued at over 27 million dollars dockside. Louisiana production generally ranks first among the Gulf States and first or second nationally. The 1985 production value at the wholesale level was 51 million dollars (NMFS 1977). At the retail level, value of the 1985 harvest increases to nearly 76 million dollars. The Louisiana oyster industry is labor intensive and, as a result, is a large employer within the coastal community. The Department of Wildlife and Fisheries annually leases approximately 1,500–2,000 tonnage licenses, 600–1,500 oyster dredging licenses and approximately 100 oyster shop and resale licenses. Additionally, this industry has an importance to Louisiana's culture and heritage commensurate with its considerable economic impact.

The oyster industry is not only of tremendous importance to the local economy but it also contributes significantly on a national scale. In 1985, the total U.S. consumption of oysters was over 90 million pounds. Of this total, 46 million pounds was imported at a probable cost of over 70 million dollars. It is anticipated that U.S. consumption of oysters will increase. As a result, a considerable decrease in Louisiana's oyster production, as forecasted, will aggravate the existing shortfall in U.S. production.

DEVELOPMENT AND ORGANIZATION OF THE INDUSTRY

Coastal Louisiana is characterized by extensive estuarine areas created over the past 5,000 years by the Mississippi River. Oyster populations have flourished and declined in the vicinity of each of the emerging and retreating deltaic lobes. While oysters have undoubtedly been exploited in this region since prehistoric times, the first commercial operations took place in the early 1800's in the estuaries near the present Mississippi River Delta. In the mid 1800's, immigrant fishermen from Dalmatia, using hand tongs, realized that high quality oysters could be produced by transferring seed from the natural reefs near the delta to bedding grounds closer to the Gulf of Mexico (Korringa 1976).

In Louisiana, the oyster fishery has developed to a large extent into a mariculture industry. Mariculture in this instance means utilization of the environment to produce a high quality product. During the 1840's and 50's, it became apparent to Louisiana fishermen that oysters obtained from certain waters had a better shape, were better tasting, larger, and consequently, were in greater demand than oysters apparently of the same age but from other locations. Those oysters became a delicacy, and the demand soon outstripped the supply. To compensate for this, fishermen began moving small oysters into those preferred growing areas. The early fishermen had enough foresight to recommend legislation which would set aside certain grounds for private culture (leased from the State), and the remaining natural reefs were placed under State control.

It is difficult to conceive of an oyster fishery based solely on public grounds. A public fishery tends to reduce the individual incentive to maintain the reefs and, in the words of Mattiessen (1970), "the fisherman is a hunter rather than a farmer". Since 1962, Louisiana's oyster grounds have been divided into two regions: State-controlled (referred to as "red line" areas), and those set aside to be leased to private individuals (Perret et al. 1970). Approximately 229,060 acres were under lease in May 1980 (Survey Section, Division of Oysters, Waterbottoms and Seafoods, LDWF), and the State under its jurisdiction approximately 800,000 acres with "red line" areas. Of those 800,000 acres, 16,453 acres are maintained within managerial sections referred to as "Seed Ground Reservations",

6,737 acres are maintained as a "Public Reef" located in Calcasieu Lake on the extreme western boundary of the State, and the remaining acres are considered "Oyster Seed Grounds". "Seed Ground Reservations", are generally entire bays spread out along the coast and are harvested on alternate years, unless biological evidence indicates otherwise. They are primarily managed for the production of seed oysters; However, if a fisherman is properly licensed and the oysters meet the legal 3-inch size requirement they can be harvested for direct sale from those grounds. The "Public Reef" located in Calcasieu Lake is utilized for handtonging only, and a harvesting limit is in effect. Of the remaining 800,000+ acres under State managerial supervision, only about 200,000 acres are fished annually for oysters.

The LDWF has legislative responsibility to manage those areas under its control and to provide a ready source of seed oysters (R.S. 56, Part VII, Sub Part D, Section 456). Commercial fisherman generally enter the "Oyster Seed Grounds" when they open in September (by law the first Wednesday after Labor Day). Those commercial fishermen who bed (transplant oysters) are primarily interested in 1- to 3-inch seed oysters which are approximately one year old. Depending on market conditions, 3-inch and above oysters may be bedded, although in the majority of cases commercial-size oysters are culled for direct sale. The seed oysters will be moved onto private bedding grounds (leases), generally in more saline waters which results in better growth, but at the same time increases mortalities from predators and disease. These oysters generally remain on the bedding grounds three to five months or longer.

The basic organization of the fishery was thus established. The State supplied the seed, and the private leaseholders transferred the seed to their leases for growth to market size. The system has endured over the years; however, the need to move large quantities of oyster seed to growing areas has lead to the development of more efficient methods of exploitation.

THE PAST

There has been a rich history to the Louisiana oyster industry, and legislation evolved as the needs presented itself developing a close relationship between LDWF and industry, starting in 1886 up to the present. The first attempt to regulate the oyster industry occurred in 1886 with the passage of a legislative act.

In 1870, because of numerous complaints that oyster reefs in coastal Louisiana were being rapidly depleted and destroyed, the Legislature passed legislature which closed the oyster season from April 1st to September 15th, and provided penalties for taking oysters.

The first concerted attempt by the State to regulate the oyster industry occurred in 1886. The act authorized the governor to appoint an Oyster Commission from each district, and also authorized the leasing of waterbottoms (three acres per person) to individuals or corporations, and established licenses enabling lessors to harvest and protect their oysters and reefs. Although State laws were in effect, enforcement was difficult because the local judiciary was responsible for apprehension and punishment, allowing destruction of local oyster reefs to continue.

An act abolished the three oyster districts in 1902 and gave individual parishes exclusive jurisdiction of the waters within each parish. This led to even greater conflicts because of competition and unmarked parish boundaries in open water areas and Enforcement continued to be ineffective because of local politics, thus compounding the problem. The act also increased to 10 acres the amount of waterbottom available for leasing to one person.

In 1900, the legislature realizing the ineffectiveness of then current oyster policy, appointed a legislative investigative commission composed of two senators and three representatives to study the industry. It was their report to the General Assembly of 1902 that resulted in the adoption of Act 153. This act created the five-member Oyster Commission of Louisiana and gave them statewide control over the industry. The commission later became the Oyster, Waterbottoms and Seafood Division, the first and therefore oldest division of the Department.

During these years, the first "shell plants" for the production of oysters occurred. Mississippi packers "planted" or deposited 45,000 barrels of oyster shells in Louisiana waters, without cost to the State of Louisiana. Additionally, 12,000 barrels were purchased by Louisiana and donated to Terrebonne and Lafourche parish fishermen as cultch material. The first plantings of shell for rehabilitation purposes in Louisiana were made by H. F. Moore and T. E. B. Pope of the U.S. Bureau of Fisheries in the years between 1906 and 1909. They made a series of experimental plantings in various bays of Louisiana using oyster and clam shell as cultch. These experiments revealed the ability to establish productive oyster reefs from shell plants.

The first impliment used by the industry was the oyster tong. They were used until 1905 when a Yugoslav immigrant developed a dredge. This dredge was connected to a hydraulic winch to facilitate lifting. The change from sailing to power vessels began in the 1920's, whereas development of water pumps to facilitate loading was begun in the early 1970's. At first water pumps were used to load, then in the latter part of 1974 the pumps were used to both load and unload oyster boats. Along with these developments came highways which facilitated the movement of more and more product. Even though the advances could be considered significant they have been too few and too slow in coming.

PRESENT

Louisiana's present average production of 12.5 million pounds generally ranks it first nationally. This production has seen an increase in the last five years. Louisiana's premier status is due primarily to the reduced production on the east coast particularly Maryland and Virginia.

The present production is not without significant problems. And they are:

1. *Predators and Parasites:* There are various predators and parasites including (but not limited to)
   The oyster drill or conch (*Thais*),
   Crabs (especially the stone crab *Menippe*),
   The black drum (*Pogonias cromis*), and
   The parasite, *Perkinsus marinus* (*Dermocystidium marinum*).
   One of the biggest predators of all, man, has also taken its toll. This is a dual problem in not only as a loss of the resource, but the thieving takes away from the incentive to relay oysters onto private leases.
   Man's involvement leads to the next problem. Saltwater intrusion causes us to move our operations further inland and there we find contamination from man's waste-water outfall.
2. *Pollution:* This is certainly one of the major problems and the area closures are increasing over the years. Thus, one has to assume that the situation is getting worse. There is also a problem with the microbiological standard and with the nonuniformity in the implementation of that standard. The industry has developed cultivation practices around the openings and closures, adopted by the State Health Department.
3. *More people, more boats, and the equipment is becoming more efficient.* You never loose a person or a boat once a new one is built; there is just an addition to the fleet. Too many dollars are chasing too few oysters.
   Louisiana's production has gone from 4 million pounds in 1900, to some 10 million pounds by 1937, and averaged 9 million pounds through 1980. This production was maintained with a small fleet of fishing vessels. Thus the individual production was quite high. However, for the last five years the average production has increased to 12.5 million pounds, with a very large increase in licensed vessels. This simply means that production has been dispersed among many more, and thus individual production in most cases has decreased.
4. *Conflict with other user groups:*
   As with virtually all of the activities in the wetlands, there are conflicts between user groups. One rather significant conflict is that between the petroleum industry and those that depend on the renewable fishery resources within those wetlands (See Soniat, this volume). Energy-related environmental damages to the oyster industry can be grouped into three categories—damages resulting from petroleum exploration, dredging associated with moving and locating drilling paraphernalia or laying of transmission lines (pipelines), and pollution associated with the industry.

Perhaps the most significant problem is the fact that we know what the problems are. We have documented the problems (Dugas 1981), various groups have discussed these problems, and a lot of money has been spent looking and talking about them. However, the problems remain.

FUTURE

Future Louisiana oyster farmers or oyster fishermen will not be operating as they presently do. They will have to change, adapt to problems, and work out solutions if they are to survive. For example, an adaptation to the pollution problem could be that instead of transplanting oysters where they are best suited now, fishermen could place them in areas that will be opened at the time of harvest. In regard to manipulating the environment more usefully, the use of freshwater diversions and barrie island reconstruction needs to be explored.

The industry also needs to further utilize research technology and oyster biology technology. This has been provided to us in the past by Wildlife and Fisheries oyster biologists and extension service agents. We need to depend more on this productive relationship. We must also utilize the technology developed in the computer industry, particularly software for recordkeeping and rapid analysis of profit/loss as it pertains to various operations of the oyster business. The technology developed for oyster hatcheries and depuration (either tank depuration or natural depuration utilizing the relay technique) needs to be utilized. More marketing techniques must be developed. There is no reason to produce the seafood products we do here in Louisiana and have limited processing. We make good money for other processors in other states.

Before we can predict the future we have to understand that the business we operate in Louisiana is similar to any other farming operation. It is dependent on nature and we should not forget that. We should try to work with nature and develop our operations around it. This dependency on nature creates feast or famine. We must change our present procedures, to different and daring ventures that are compatable with the waters we are forced to work in, the regulations we are forced to work under and the increasing competition we are faced with.

I would, however, like to conclude with a personal note in regard to the Pausina Corporation's future. My number 1 son is a chef in Chicago, my number 1 daughter has a

masters degree in education and is presently teaching, and my number 2 son is undecided. This is imply an indication that future generations of potential oyster farmers might be less inclined to venture into the business.

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ABSTRACTS OF TECHNICAL PAPERS

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MOLLUSCAN DISEASE

DISEASES OF CULTURED MOLLUSCS IN BRITISH COLUMBIA, CANADA. Susan M. Bower, Department of Fisheries and Oceans Pacific Biological Station, Nanaimo, British Columbia, Canada.

To date, four infectious organisms, a bacterium and three protozoans, that cause disease and mortalities in cultured molluscs have been identified. Nocardiosis in Pacific oyster (*Crassostrea gigas*), caused by an actinomycete bacterium, is manifested as focal green pustule-like lesions. Infected oysters were found in all seasons from 5 localities and although many oysters succumb to the infection during the fall, field data suggest that some infected oysters can survive. Similar lesions are induced by an intracellular protozoan commonly known as a microcell. Active microcell infections have only been observed in the spring when mortalities of large, older oysters at the low tide level can exceed 50%. Infected oysters have been found in 6 localities, 3 of which also yielded oysters with nocardiosis. However, dual infections in a single oyster were rare. The second protozoan, a thraustochytrid parasite, recently named *Labyrinthuloides haliotidis*, has only been observed in cultured juvenile abalone (*Haliotis kamtschatkana* and *H. rufescens*) less than 4.0 mm in shell length. However, this parasite can kill the majority of 100,000 small abalone in a raceway within 2 to 3 weeks. The third protozoan was encountered for the first time in the spring of 1988 in experimentally cultured Japanese scallops (*Patinopectin yessoensis*). The form within the scallop is *Perkinsus*-like and it occurs in the connective tissues of all organs. Within two months at one grow-out site, about 40% of the scallops succumbed to this parasite.

GROWTH AND SURVIVAL OF HATCHERY PRODUCED MSX RESISTANT OYSTER STOCKS IN DELAWARE BAY. John W. Ewart, College of Marine Studies, University of Delaware, Lewes, Delaware; **Richard Cole** and **Jeff Tinsman,** Delaware Department of Natural Resources and Environmental Control, Dover, Delaware.

The Delaware Sea Grant Marine Advisory Service and Department of Natural Resources and Environmental Control (DNREC), with the cooperation and assistance of the Rutgers Shellfish Research Laboratory, have been monitoring the growth, survival, and MSX activity in oysters produced from MSX resistant broodstock at an experimental planting site in Delaware Bay. In October 1986, seed oysters produced from Rutgers strain (Bx2FA) and resistant native stocks (20% inbred; 80% outcrossed) were planted on a one acre test plot in Delaware Bay. Naturally-set 1986 year-class oysters from New Jersey's Shell Rock seed bed were transplanted to an adjacent one acre site as a control. Results through the first growth season (spring–fall 1987) established that there were distinct differences in growth, survival and disease activity between the two groups. Average growth increase was 24% higher in the resistant stock oysters and disease related mortality was less than half that of the natural stock control (19% vs. 43%). Resistant stock oysters were also found to have a lower degree of MSX activity and a markedly lower percentage of systemic infections. Results from the second growth season (spring–fall 1988) thus far support last year's observations. Data from both years of the study are presented and discussed along with recommendations for further research.

A REGIONAL ATTACK ON THE MSX PROBLEM THROUGH GENETIC SELECTION AND MANIPULATION OF OYSTER STOCKS. Susan E. Ford and **Harold H. Haskin,** Shellfish Research Laboratory, Rutgers University, P.O. Box 687, Port Norris, New Jersey.

The recent spread and intensification of MSX disease, caused by the protozoan parasite *Haplosporidium nelsoni*, has caused severe mortalities of oysters, *Crassostrea virginica*, in the northeastern United States from Cape Cod to Chesapeake Bay. A consortium of universities and aquaculture businesses (Rutgers University; Universities of Maine, Connecticut, Delaware, and Maryland; Aquacultural Research Corp. and Cotuit Oyster Co.), with funding from the Northeast Regional Aquaculture Center, has begun an attack on the problem by use of genetic selection and manipulation. The goal is to produce oyster strains that will be useful to aquaculturists throughout the Northeast region. Industry needs are disease resistance (to "Dermo" [caused by another parasite *Perkinsus marinus*] and to MSX disease) as well as rapid growth, high meat yields, and uniform quality whether or not disease is present.

The preliminary phase of the project is to test existing MSX disease-resistant strains (developed by Rutgers University through selective breeding in Delaware Bay) in several other Northeast locations. Growth and survival of these strains will be compared to local stocks under different temperature and salinity regimes, when challenged by *H. nelsoni* and *P. marinus*, and when under little or no pressure from either disease. Results will suggest future breeding strategy—specifically whether existing Rutgers strains do as well in other areas as they do in Delaware Bay or whether hybridization with local stocks might improve performance.

Other facets of the project include determining whether polyploidy improves disease resistance, and research into genetic, physiological, and cellular mechanisms involved in resistance. Preliminary results on survival, growth, disease levels, and meat quality of Rutgers strains and local stocks tested on Cape Cod and in Delaware and Chesapeake Bays will be presented. This is NJAES Publication No. K-32901-1-88.

RECENT CHANGES IN THE RANGE OF "MSX" *HAPLOSPORIDIUM NELSONI*. Frederick G. Kern, National Marine Fisheries Service, Northeast Fisheries Center, Oxford, Maryland.

In 1957, MSX (*Haplosporidium nelsoni*) was recognized by Drs. Haskin, Stauber, and Mackin as the agent devastating the

oyster (*Crassostrea virginica*) populations of Delaware Bay. By 1959, *H. nelsoni* had spread to the waters of Chesapeake Bay with similar results. A review of published literature and unpublished data collected from 1960 to 1980 indicates the range of the disease to be from southern New England to North Carolina. *H. nelsoni* is again causing major losses to east coast oyster populations. New data and recent reports extend the range of *H. nelsoni* from Maine to Florida.

Possible explanations as to when and how the range extension occurred will be discussed.

HEMOCYTE AND HUMORAL ACTIVITIES OF TWO POPULATIONS OF OYSTER (*CRASSOSTREA VIRGINICA*). Jerome F. La Peyre and **Fu-Lin E. Chu,** Virginia Institute of Marine Science, School of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Mobjack Bay oysters are considered to be relatively MSX resistant after continuous selection over two decades by high mortalities. James River oysters are highly susceptible to diseases when transferred to areas enzootic for *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX). Hemocyte activity in terms of chemotaxis and chemiluminescence, and the humoral activity (hemagglutination) of oysters from these two areas are compared. Zymosan was used as a stimulus for both chemotaxis and chemiluminescence assays. Sheep red blood cells are used to quantify hemagglutination. Results indicate the following: There is no difference in differential hemocyte counts between Mobjack Bay and James River oysters. Total cell counts for Mobjack Bay oysters ($1.5–5.46 \times 10^6$ cells/ml, $2.76 \times 10^6 \pm 1.82$) are higher than for James River oysters ($0.61–1.52 \times 10^6$ cells/ml, $0.90 \times 10^6 \pm 0.43$). Similarly, Mobjack Bay oyster hemocytes showed higher chemotaxis activity (15.0–40.2% chemotaxis, 28.5 ± 13.0) than did James River oyster hemocytes (4.4–19.6% chemotaxis, 9.0 ± 7.8). The agglutination titers of sera from Mobjack Bay oysters (4–256, 160 ± 120) were also higher than James River oysters (8–64, 50 ± 28). The chemiluminescence response of hemocytes from these two oyster populations appeared to be similar. Experiments will be repeated using *Escherichia coli* as the stimulus.

METHODS OF REDUCING THE IMPACT OF MSX UPON SMALL-SCALE OYSTER CULTURE OPERATIONS. George C. Matthiessen, Ocean Pond Corporation, Fishers Island, New York.

Increasing incidence and intensity of oyster (*Crassostrea virginica*) mortalities in New England resulting from MSX (*Haplosporidium nelsoni*) infections require adjustments in culture methods. Such adjustments might include reducing the period of exposure on infected beds, concentrating upon hatchery production of disease-resistant stock, and genetic manipulation that might result in an increase in growth rate as well as improved levels of disease resistance. Certain of the difficulties encountered by small-scale culture operations in adopting these measures are discussed.

***PERKINSUS MARINUS*; DISTRIBUTION IN ATLANTIC AND GULF COAST OYSTER POPULATIONS WITH SUGGESTED CONTROL METHODS. Sammy M. Ray** and **Daryl E. Anderson,** Marine Biology Department, Texas A&M University at Galveston, Galveston, Texas.

Recent surveys show that *Perkinsus* (*Dermocystidium*) *marinus*, a lethal protozoan parasite of the American oyster (*Crassostrea virginica*) is widely distributed in oyster populations on the Atlantic coast from Chesapeake Bay to Georgia and on the Gulf coast from the Florida Everglades to Brownsville, Texas. *Perkinsus* is most prevalent and causes significant oyster mortality during the warm months in areas where the water salinities consistently exceed 20‰. The current drought along with higher than usual summer temperatures can be expected to exacerbate both the spread and intensity of *Perkinsus* infections.

In Chesapeake oyster populations, winter temperatures usually reduce parasite infections to levels that are undetectable with available assay procedures. Gulf oyster populations, on the other hand, show reduced infection intensity in winter but the parasite remains detectable throughout the year. Thus the moderating effect of low winter temperatures, which provides some protection for Chesapeake oysters from *Perkinsus* disease, does not prevail in the Gulf. For this reason, the strategies for developing control measures for reducing this oyster disease on the Gulf coast will be different and more difficult than those applicable to the Chesapeake Bay. Currently employed and potential measures for reducing *Perkinsus* disease in Gulf and Atlantic oyster populations will be discussed.

QUAHOG CULTURE: STATE OF THE ART

A BRIEF HISTORY OF CLAM CULTURE IN THE U.S. Michael Castagna, College of William and Mary, Virginia Institute of Marine Science, Wachapreague, Virginia.

Clam culture, especially of *Mercenaria*, has become a relatively important industry in the U.S. in recent years. William Firth Wells described culturing clams along with several other commercially important species in 1926. It was not until the mid-1950's that a commercial clam hatchery and growout were established by Richard L. Kelly near the town of Atlantic, Virginia, followed a few years later by a hatchery in West Sayville, New York by Joseph Glancy. By December 1978 when the National Aquaculture Plan was being developed, there were less than 10 clam culture operations in the U.S. Today there are more than 85 clam farms and more than two dozen hatcheries producing clam seed for nursery and growout operations. These range in size from small one-family operations to well financed clam farms with large production capacities.

A TOUR OF THE FACILITIES OF INDIAN RIVER MARICULTURE OF NEW YORK, INC. Paul E. Chanley, Indian River Mariculture of New York, Inc., P.O. Box 12, Grant, Florida.

Indian River Mariculture, Inc. was founded in 1980 to raise clams (*Mercenaria mercenaria*) in the Indian River in Florida about halfway between Miami and Jacksonville. In 1987, the company was purchased by Indian River Mariculture of New York, Inc. The present company has about 15 employees and is now producing both clams and oysters (*Crassostrea virginica*). This presentation is a narrated VCR tour of our facilities showing our "brown water" hatchery, wellers, grow-out trays and the specialized handling equipment used in caring for and harvesting crops.

HARD CLAM CULTURE AT AQUACULTURAL RESEARCH CORPORATION. Richard A. Kraus, Aquacultural Research Corporation, P.O. Box AC, Dennis, Massachusetts.

The goal of Aquacultural Research Corporation (ARC) is the rearing and marketing of mature stocks of the hard clam (*Mercenaria mercenaria*) and the oyster (*Crassostrea virginica*) in an economically viable manner. To accomplish this goal, ARC maintains a shellfish hatchery, operating on a year round basis, and growout sites in the waters of Cape Cod Bay, Massachusetts. In addition to providing seed for our own growout program, the hatchery is a major supplier of seed to other private and public entities for growout. The hard clam stock reared by ARC is the result of a selective breeding program begun in 1974, with growth rate being the main selection criterion. In addition, the brown shell markings characteristic of the hard clam notata variant were bred into ARC stock to distinguish ARC cultured stock from wild local stocks. The breeding program has resulted in growth to market size approximately 40% faster than local wild stock and additionally has been shown to perform well over a wide geographic range.

Field growout of hard clams by ARC is a two step process involving one growing season within protective nursery cages and then planting on-bottom using a coarse plastic mesh for predator protection during final growout to market size. Recovery rates average 80% for the nursery cage phase and 65% for the bottom plant phase. Overall growout time at our sites is 24–28 months, starting with a spring planting of 5 mm. During the past three years, ARC has harvested commercial scale (>100 metric tons) quantities of hard clams from its growout sites.

HARD CLAM (*MERCENARIA MERCENARIA*) SEED PRODUCTION. Steve Malinowski, The Clam Farm, Inc., Box 402, Fishers Island, New York.

The Clam Farm, Inc. of Fishers Island, N.Y. utilizes a low-cost, low-technology four stage system for producing 20 mm hard clam (*Mercenaria mercenaria*) seed. Hatchery production and growth to 5–7 mm are accomplished in a combined outdoor, land-based facility. The hatchery consists of two 400 liter conicals enclosed by a 1.4 × 2.5 × 1.4 m solarium. A removable insulated (R-19) plywood cover encloses the entire solarium. This system allows for excellent temperature control (24° ± 2°C) even in early May when evening air and ambient water temperatures may range from 10–14°C. Post-set animals are held in a downflow system in conicals for a week after metamorphosis and then introduced into the passive upflow system at a size of 400–500 microns. The passive upflow system consists of eight 0.7 × 0.7 × 2.5 m plywood troughs containing a total of 56 silos (35 cm diameter). Two pumps (¾ and 2 h.p.) provide 420–560 l/min. of ambient bay water which results in a flow rate of 15–20 l/min./silo. The system design incorporates passive water reuse. After attaining 5–7 mm (July–August), clams are planted in 0.7 × 1.4 m bottom trays with plastic mesh covers and a coarse sand substrate. Clams range from 7–12 mm by the end of the first growing season (mid-October) and overwinter in the bottom trays. The following May, clams are removed from bottom trays and planted in 1.5 × 3.0 m plots of mesh and crushed stone. These plots consist of a bottom layer of mesh covered with 2.5–5.0 cm of crushed stone with a protective top mesh anchored down with a reinforcement bar frame. In October, clams have attained a size of 20 mm and are removed from the mesh/gravel plots.

FIELD NURSERY CULTURE AND GROWOUT OF HARD CLAMS, *MERCENARIA*, IN COMMERCIAL SCALE AQUACULTURE SYSTEMS. John J. Manzi, Colden Battey, N. H. Hadley and **Marc Carter,** South Carolina Marine Resources Research Institute, Charleston, South Carolina.

Techniques for the field nursery culture and growout of hard clams have been developed and tested in South Carolina over the last eight years. Two methods:

1. The use of vacant shrimp ponds for nursery culture, and
2. intertidal pen culture for growout to market size, have emerged as reliable and economic techniques for commercial culture.

It has been successfully demonstrated that relatively high densities (≥21,600/m²) of small clam seed (1.4–4.5 mm) can be reared in shallow trays and on mesh covered pond bottoms during the shrimp pond vacancy period (November–April) in South Carolina. Depending on seed size and density, growth in ponds ranged between 0.6–1.5 mm/month with consistently low mortalities. It has also been demonstrated that larger seed (8.0–10.0 mm) produced through standard land based upflow nursery culture can be successfully grown to market size (45–50 mm longest dimension) in intertidal pens. These pens (2.0 m wide × 10.0 m long × 1.0 m high), constructed of 1.25 cm square vinyl coated wire, have been routinely used to rear seed at planting densities of 800–1,600 clams/m², yielding average harvest of 430–800/m². These techniques in conjunction with land based upflow nursery culture, have established an economical and efficient methodology for the commercial culture of hard clams in South Carolina.

BIVALVE SEED PRODUCTION BY A COMMERCIAL HATCHERY/NURSERY USING A MAINE ESTUARY. William H. Mook, Mook Sea Farm, Inc., H.C. 64 Box 041, Damariscotta, Maine.

Mook Sea Farm, Inc. located on the Damariscotta River in South Bristol, Maine, produces seed clams, oysters, and scallops for sale to commercial growers and shellfish management programs. Hatchery production for 1988 is expected to exceed 60 million animals. Microalgae production for the hatchery is compact and efficient, with cell densities in batch cultures routinely exceeding 30 million cells/ml. Post-set shellfish are grown to sizes ranging from 0.5–3 mm before sale or transfer to a nursery.

A typical land-based upflow nursery is located at the hatchery. Since ambient water temperatures at the hatchery rarely exceed 20–21°C, this nursery is used for growing species which do well at cooler temperatures or for growing warmer water species more slowly in order to maintain a larger size range of high quality seed available for sale. Mook Sea Farm has successfully developed a new type of upflow nursery which employs tidal currents instead of electricity. This tidal nursery consists of an upwelling tank with an open scoop at one end, suspended beneath a 20 ft. × 12 ft. raft. Since the raft is on a single point mooring and has a large tank suspended beneath it, the tidal scoop is always oriented into the tidal flow and water is forced up through bins, each containing a layer of juvenile shellfish. This nursery allows for rapid growth of very small oyster and clam seed (1.0 mm) by taking advantage of warmer water temperatures found at the landward end of the Damariscotta River estuary. Juveniles can be grown in the tidal upweller to a size large enough (3–5 mm) for transfer to floating trays.

CLAM CULTURE: STATE OF THE ART IN FLORIDA, U.S.A. David E. Vaughan, Mollusc Culture Department, Division of Applied Biology, Harbor Branch Oceanographic Institute, Fort Pierce, Florida.

Clam culture techniques have developed quickly in Florida. Some are adaptations of existing technologies from other areas, and many are new technologies developed for the Florida environment. High growth rates are advantageous, but high fouling rates, high temperatures, and heavy predation contribute to disadvantages and necessitate different culture techniques.

Land nursery techniques are similar in the form of raceways or upwelling systems, but one closed system raceway uses shrimp farm effluent to raise small seed to large seed, and to harvest size. Other land based systems using cultured algae or natural phytoplankton are being developed. Field based systems have had the most success, using trays, or bags with and without substrate. Small seed (>300 μm) have had good success in floating upwellers and small mesh bags in cages. A shellfish growing belt system designed for oyster grow-out shows potential use as a clam nursery system that can be handled easily and mechanized.

Field grow-out techniques of trays or bottom nets have taken into account the fouling pressures or the predator pressures in their adaptive handling schedules and materials used. Bottom planting nets have been used for planting of over 10 million clams and preditor control and harvesting methods for these large numbers have been devised. Double layered bottom nets (or the "soft tray") has potential for field grow-out and has been very successful for field nurseries. The influence of over 70 farms planting clams in 1987 and more expected in 1988, has led to the quick development of varied clam culture technologies.

AQUACULTURE TECHNIQUES

PRINCIPLES OF MARINE FARM ENGINEERING. John A. Benson, John S. Leonard, Edward C. Braden and **Michael Neushul,** Neushul Mariculture Inc., 475 Kellogg Way, Goleta, California.

The successful operation of a marine farming industry will depend on a set of sound engineering principles. During the past four years, we have moved from an observational, trial-and-error approach to ocean farm design to one where hydrodynamic measurements are used systematically to answer specific questions about the siting, design and operation of marine farms. The net water motion experienced by an organism on a marine farm is a combination of two things: the available water particle motion due to the waves and currents present and the motion of the structure, which is itself a controllable structural response to the hydrodynamic loading. We have used spectral analysis to measure frequency-dependent changes in the water velocity over the crop that result from experimental alterations of two basic farm designs, long-line and simple anchor-buoy systems.

Our new scientific testing and analysis protocol led us to the discovery that compliant marine farms can be "tuned" to use wave energy of selected frequencies to enhance or reduce water flow over the crop. Flow enhancement was occasionally very high: in four tests, water flow measured on the farm exceeded even the ambient flow expected in the absence of the farm. Our measurement protocol and the design principles, such as tuning, that we are developing should ultimately provide the technical basis for the future design of marine farms for many crops and locations.

TECHNIQUES FOR THE COMMERCIAL SCALE INDUCTION OF METAMORPHOSIS IN QUEEN CONCH *STROMBUS GIGAS* (L.) LARVAE. Megan Davis, William D. Heyman and Wilbert Harvey. Caicos Conch Farm, 7600 S.W. 87th Avenue, Miami, Florida.

Intensive Queen Conch *Strombus gigas* (L.) mariculture requires a routine, inexpensive, and effective process for the induction of metamorphosis of veligers. Larvae are routinely cultured to metamorphic competence in 22 ± 3 days at the Caicos Conch Farm, Turks and Caicos Islands. Extract of *Laurencia poteii* has been successfully used for the past 5 years as a metamorphic in-

ducer, producing an average of 83% recovery in 1988, with an average growth rate of 0.20 ± 0.04 mm/day post induction. There are inherent variations, and costs involved with using *Laurencia* extract for the induction of metamorphosis. The goal of this research is to determine if Potassium Chloride (KCL) can replace *Laurencia* extracts with less variations, lower costs and equal recovery and health of post-induction conch. Preliminary results indicate that 6h, 8h, and 10 h. exposures to 15 mM KCL in seawater, produces 71–84% recovery of veligers with an average growth rate of 0.20 ± 0.02 mm/day post induction.

INCREASING GROWTH RATES AND SURVIVAL OF GIANT CLAMS IN MARICULTURE. William K. Fitt, Department of Zoology, University of Georgia, Athens, Georgia.

Giant clams of the family Tridacnidae are unique among animal species in mariculture in that they have an internal food source in the form of symbiotic algae (zooxanthellae of the genus *Symbiodinium*) that provide a significant portion of their nutrition. Recent efforts to improve growth and survival rates of tridacnids have centered on selection of species and strains of *Symbiodinium* and additions of inorganic nutrients. Results show that some strains of *Symbiodinium* living in symbiosis with *Tridacna gigas* and *Hippopus hippopus* yield growth and survival rates of clams 3–5 times those of symbioses with other strains. When inorganic nitrogen in the form of ammonia is added, growth rates of clams almost double compared to controls.

OBSERVATIONS ON GROW OUT SYSTEMS FOR THE SOUTHERN BAY SCALLOP, *ARGOPECTEN IRRADIANS CONCENTRICUS*. Peter B. Heffernan, Randal L. Walker and **John W. Crenshaw,** University of Georgia Marine Extension Service, P.O. Box 13687, Savannah, Georgia; **Joe Hoats,** Waddell Mariculture Center, P.O. Box 809, Bluffton, South Carolina; **David E. Vaughan,** Harbor Branch Oceanographic Institute, Inc., 5600 Old Dixie Highway, Fort Pierce, Florida.

Fouling, mainly due to heavy oyster spatfall, severely limits the viability of bay scallop natural grow out systems in Georgia. However, in an effort to provide insights into possible viable alternatives for culture of this species, several land based as well as natural grow out systems have been examined in cooperative studies in Georgia (GA), Florida (FL), and South Carolina (SC). Land based sytems included miniature ponds (GA—pearl net culture), ¼-acre polyculture (with penaeid shrimp) pond systems (SC—pearl net and floating cage cultures), and upwelling systems (FL). Natural grow out systems included pearl net culture in a sheltered intertidal creek (GA), an exposed river (GA), and sheltered upwelling systems (FL).

Simultaneous pond culture trials at the Skidaway Island (GA) and Waddell Mariculture Center (SC) facilities showed an approximate tripling in size within a 10-week period (June 27–August 5, 1988) ($\bar{x}$ increasing form *ca* 11–33 mm) with pearl net and floating cage culture (778/m^2). The GA pearl net trials yielded significantly larger scallops than their counterparts in SC, while pearl nets produced significantly larger scallops than the floating cage system (SC). Both pond systems supported significantly higher growth rates than were observed in pearl net cultures studied in an intertidal marsh creek (GA). Pond trials (GA) yielded significantly larger scallops than the river trials, which were not significnatly different from the SC tests. Mean survival rates (10-weeks) were commercially acceptable at all sites (≥65%). Preliminary results from the Harbor Branch Oceanographic Institute (FL) indicate significantly higher growth rates in natural versus land based upwelling systems.

QUAHOG BIOLOGY

SPECIES DISTRIBUTIONS IN HARD CLAMS (GENUS *MERCENARIA*): COMPLEX PATTERNS REFLECT NATURAL PROCESSES AND THE INFLUENCE OF MAN. Theresa M. Bert, William S. Arnold and **Hector Cruz-Lopez,** FDNR, Marine Research Institute, 100 Eighth Ave., S.E., St. Petersburg, Florida.

Electrophoretically detectable variation in 17 protein loci was used to determine the evolutionary relationships of clams of the genus *Mercenaria* in the eastern U.S.A. and California. Allele frequencies showed that *M. mercenaria* is distributed along the Atlantic coast in shallow-water inshore areas and *M. campechiensis* is apparently distributed offshore in the Atlantic and throughout the Gulf of Mexico. Superimposed on this general distributional pattern are a number of geographically distinct, disjunct regions where the two species co-occur. The degree of interbreeding between the two species varies widely among these regions. In addition, some pure species populations exhibit patterns of allele frequencies quite distinct from those observed to be characteristic of the species. Finally, allele frequencies at some loci vary clinally within species, and in *M. mercenaria*, heterozygosity generally increases with movement southward in the Atlantic. The complex and mosaic patterns of species distribution, allele frequency variation, and hybridization seen in hard clams are apparently the product of the combined effects of geological and climatic events, local adaptation, present hydrographic regimes, and man's activities.

GROWTH OF THE HARD CLAM IN GROW-OUT CAGES IN COASTAL GEORGIA. John W. Crenshaw, Peter B. Heffernan, and **Randal L. Walker,** University of Georgia, Marine Extension Service Shellfish Laboratory, Skidaway Island, P.O. Box 13687, Savannah, Georgia.

As part of a genetic selection program for increased growth rate in the hard clam, *Mercenaria mercenaria*, several cohorts of young were initiated by spawning locally collected stock in 1986. Two cohorts, spawned on April 14 (A) and May 8 (B), metamor-

phosed at 18 and 19 days respectively and were maintained in laboratory raceway downweller systems until December 2, 1986 when they had attained mean shell length of 7.76 mm (A) and 3.98 (B). Clams were then transferred to divided wooden tables (4 × 4′) with 4″ sides covered with vinyl covered wire mesh at densities of from 1750–3450 clams per table, and then placed in a tidal creek. Measurements were taken at irregular intervals until July 21, 1987 when surviving clams of cohorts A and B were divided each between two tables to reduce density. On March 16, 1988 all clams of cohort A were brought into the laboratory for measurement and selection of parents of the first selected generation. Replicates (N = 842 and 390) had attained mean shell lengths of 31.10 mm and 33.01 mm respectively. On April 25, measurements of two replicates of cohort B revealed that a random sample of one replicate (N = 400) had attained a mean shell length of 32.78 mm; the other replicate (N = 228) had a mean shell length of 32.60 mm. Mean rates of growth varied from 1.51–1.71 mm per month with both replicates of cohort A, put into grow-out at a larger size than those of cohort B, growing at a slightly lower rate.

REPRODUCTIVE ISOLATION BETWEEN THE HARD CLAMS, *MERCENARIA MERCENARIA* AND *MERCENARIA CAMPECHIENSIS*, IN THE INDIAN RIVER LAGOON, FLORIDA. Robert T. Dillon, Jr., Department of Biology, College of Charleston, Charleston, South Carolina; **John J. Manzi,** Marine Resources Research Institute, P.O. Box 12559, Charleston, South Carolina.

The hard clam species, *Mercenaria mercenaria* and *M. campechiensis*, have traditionally been distinguished by minor morphological criteria: shell ridges, nacre color, and lunule shape. Because they rarely co-occur in the wild, and seem to hybridize with ease when they do, it has been suggested that they are only subspecies or forms. We sampled putatively pure populations of these two species and showed that they differ at seven enzyme loci, as well as in the thickness of shell ridges and nacre color. The difference in lunule shape was not striking, but when lunule height and width were included with four other shell measurements, accurate morphometric discrimination between the species was possible. We then used morphological criteria to sort clams collected from the Indian River Lagoon on the Atlantic coast of Florida, an apparent hybrid zone. Individuals with thick ridges, white nacre and/or *campechiensis*-like morphometrics had significantly different allele frequencies at most enzyme loci from individuals with thin ridges, purple nacre, and/or *mercenaria*-like morphometrics, as predicted from the pure populations. Our Indian River sample seemed to contain only about 0.5% pure *M. campechiensis* and 12% pure *M. mercenaria*, with the remainder hybrids. But the presence of some reproductive isolation in sympatry confirms the specific status of these two taxa.

***IN SITU* OBSERVATIONS OF HARD CLAM ACTIVITY AND SIMULTANEOUS MEASUREMENTS OF SHORT-TERM ENVIRONMENTAL VARIABILITY. Stephen R. Fegley, Bruce A. MacDonald** and **Timothy R. Jacobsen,** Rutgers Shellfish Research Laboratory, P.O. Box 687, Port Norris, New Jersey.

Several studies have indicated that variability in growth of suspension-feeding bivalves is related to interactions of local, site-specific environmental variables. These findings place an emphasis on collecting qualitative and quantitative, *in situ* measures of environmental variables over time for discrimination of which combinations of factors are important and how they influence bivalve growth. In the present study, intensive field sampling was made of water temperature, current speed, particulate concentration, and suspended particle size distributions over most of a tidal cycle while simultaneously observing the activity of hard clams (*Mercenaria mercenaria*, L.) located in the same area. In addition, analyses of chlorophyll, percent organics, lipids, total carbon, and energy content of the suspended material were made on samples collected throughout the tidal study. This array of environmental measures in combination with the observations of hard clam activity (extension and retraction of the siphons to the sediment surface) provide a detailed description of the conditions experienced by hard clams at the site examined.

OYSTER GENETICS AND BIOLOGY

AN INTEGRATED MODEL OF OYSTER SETTLEMENT AND METAMORPHOSIS. Steven L. Coon and **Dale B. Bonar,** Department of Zoology and Center of Marine Biotechnology, University of Maryland, College Park, Maryland; **William Fitt,** Department of Zoology, University of Georgia, Athens, Georgia.

Research from our laboratory over the last several years has led to the formulation of an integrated model of the environmental and physiological processes involved in controlling oyster settlement and metamorphosis. The larval nervous system is believed to be the central element controlling these processes. The model includes two serial control pathways: a dopaminergic behavioral (settlement) pathway and an adrenergic morphogenetic (metamorphosis) pathway. The mechanisms by which larvae respond to chemical inducers such as L-DOPA, epinephrine and ammonia, as well as biological inducers such as bacteria and other oysters, are included in the model. The roles of both soluble and surface-bound environmental factors in oyster setting are also addressed. Acquisition, during development, of competency to settle and metamorphose are separated temporally. As larvae delay settlement and metamorphosis in the absence of environmental cues, their response thresholds for these stimuli decrease. Much of the

control over the complex behaviors associated with settlement is incorporated into a hypothetical construct within the larval nervous system termed the "Integration Center." This model integrates our current understanding and provides a framework for formulating and testing additional hypotheses about the control of oyster settlement and metamorphosis. Facets of this model may be applicable to the control of matemorphosis in other invertebrate species and may enhance our ability to manipulate commercial species in culture.

PHYSIOLOGY AND ENERGETICS RELATING TO WEIGHT LOSS AND GLYCOGEN UTILIZATION DURING STARVATION IN DIPLOID AND TRIPLOID PACIFIC OYSTERS. Jonathan P. Davis, School of Fisheries, University of Washington, Seattle, Washington.

Diploid and triploid Pacific oysters were starved for 130 days in the laboratory to determine differential survivorship, and rates of weight loss and glycogen utilization during the course of starvation. Diploid and triploid oysters were reproductively active at the beginning of the experiment (July 1977), although diploids were devoting considerably more energy to reproduction than were triploid oysters. Glycogen levels were initially higher in triploid oysters.

Results indicate that when 50% of the experimental oysters had died (day 130), diploid survivors were more numerous than triploids, demonstrating a higher mortality rate for triploids under starvation conditions. The percentage of triploid oysters decreased from 69% at the beginning of the experiment to 31% after 130 days. Initial weight loss (measured as change in condition), and reduction in glycogen content in triploids exceeded that of diploids.

These results are discussed with reference to the costs of reproduction and change in body component indices during starvation and stress in bivalve molluscs.

COMPARING ADULT PERFORMANCE OF DIPLOID AND TRIPLOID MONOSPECIFIC AND INTERSPECIFIC *CRASSOSTREA* HYBRIDS. Sandra L. Downing, School of Fisheries, WH-10, University of Washington, Seattle, Washington.

A complete factorial design was used in 1986 to produce diploid and triploid monospecific and interspecifc hybrids between *Crassostrea gigas* and *C. rivularis*. The crosses were planted in Washington and California. When the oysters were stolen in California during Feburary of 1988, the Washington oysters were transferred from a mud bottom culture site to a secure dock. To evaluate the adult performance, we sampled 8–15 oysters from all the available crosses once in December 1987 and then monthly from June to October 1988. Sampling is incomplete at this time, but the preliminary results suggest the following.

Triploid percentages of spat and adutls were not significantly different except for the monospecific *C. rivularis* cross, in which they rose form 55 to 77%. While growing on long lines in California or suspended off the dock, all the crosses grew equally. However, bottom culture favored those crosses containing at least two chromosomal sets from *C. rivularis*.

Unlike interspecific salmonid crosses which are sterile, the diploid hybrids matured. In fact, a second generation was successfully produced from the original *C. gigas* (female) by *C. rivularis* (male) cross. Furthermore, a backcross with *C. gigas* was viable. Similar to earlier studies, triploids devoted less effort to reproduction and consequently had significantly higher glycogen levels than diploids during gametogenesis. Diploid *C. rivularis* had higher glycogen levels than did *C. gigas* and the two hybrids were intermediate. The difference in glycogen levels among the triploid crosses appears to be less distinct.

So far, the sex ratios have been different among the crosses: at one extreme, *C. rivularis* has yielded 100% males while the diploid *C. gigas* has been 55% female and 45% male. The hybrids have been intermediate with the triploid *C. rivularis* by *C. gigas* being 85% male and the diploid cross lower at 78% male. The diploid *C. gigas* by *C. rivularis* cross has been closer to the *C. gigas* cross with 60% male.

The aquaculture potential of the crosses will be discussed.

CELL FUSION IN THE PACIFIC OYSTER, *CRASSOSTREA GIGAS*: TETRAPLOIDS PRODUCED BY BLASTOMERE FUSION. Ximing Guo, William K. Hershberger, Kenneth K. Chew, Sandra L. Downing and **Paul Waterstrat,** School of Fisheries, WH-10, University of Washington, Seattle, Washington.

Research in our laboratory on the production of tetraploid oysters has been focused on the use of cell fusion techniques. In earlier reports we reported that tetraploids may be produced by polyethylene glycol (PEG) induced fusion of oocytes. However, the oocyte fusion technique requires removal of the vitelline membrane by enzyme treatment, a process which is tedious and often yields unpredictable results. At the two-cell stage of embryonic development, the cytoplasmic membranes of the blastomeres are in close contact, and the fusion of two blastomeres may also result in the production of tetraploids. This report presents results of research investigating the use of PEG treatment to induce the fusion of two blastomeres to produce tetraploid oysters.

Eggs and sperm were obtained by stripping conditioned adult oysters and fertilization was conducted in artificial seawater (ASW). After the majority of the developing embryos reached the two-cell stage, they were treated with 50% PEG (w/w in ASW) for 1, 2, and 5 minutes. Treated embryos were rinsed with ASW and then cultured in natural seawater. Fusion of the blastomeres was assessed by microscopic examination. Analysis of chromo-

some preparations from trochophore larvae revealed 1–4% tetraploidy. The highest level of tetraploid production occurred in the 2-minute treatment group. Additional studies are being conducted to refine the treatment procedures and to increase the yield from a very promising approach to tetraploid production in Pacific oysters.

PEDIGREED BROODSTOCKS FOR CULTURE AND BREEDING OF PACIFIC OYSTERS. Dennis Hedgecock and **Fred Sly,** Bodega Marine Laboratory, University of California, Bodega Bay, California; **Ken Cooper,** Coast Oyster Co., Quilcene, Washington; **Bill Hershberger** and **Ximing Guo,** School of Fisheries, University of Washington, Seattle, Washington.

To a large extent, domestication involves changes in human behavior that make possible breed development and improvement. Most fundamental are the assignment of economic value to the species, to particular traits, and to individual broodstock, and the keeping of pedigrees, without which breeding value cannot be judged and loss of genetic diversity through accidental inbreeding is likely.

Though the life cycle of cultivated Pacific oysters is controlled, most of the human behaviors conducive to domestication and improvement are still absent. Parts of this problem are being addressed by a collaborative research project funded by the USDA's Western Regional Aquaculture Consortium (WRAC), involving the University of California, the University of Washington, and Coast Oyster Co.

The objectives of the WRAC project are to produce and maintain a pedigreed broodstock and to partition variability in the growth and sexual maturation of this stock into genetic and environmental components. Five experimental crosses, two of 8♂ × 3♀ factorial and three of 8♂ × 3♀ hierarchical mating design, yielding a total of 120 families, have been completed. Starch gel electrophoresis of polymorphic allozyme markers is being done to confirm parentage of all families. Progeny from most of these crosses have been set on cultch, randomized on long lines, and deployed to growout areas in Puget Sound, Washington, and Humboldt Bay, California. Data on size at the end of the first growing season and estimates of genetic and environmental components of variance will be presented.

Pedigreeing is difficult and will necessitate changes in commercial husbandry practices. Industry must cease mass spawning, admixing of spawns at all phases of growout, and haphazard selecting of broodstock in order to make progress towards domestication.

THE ESTABLISHMENT OF INTERTIDAL POPULATIONS OF *CRASSOSTREA VIRGINICA* IN THE YORK RIVER, VIRGINIA: A RESULT OF SETTLEMENT OR RECRUITMENT? G. Curtis Roegner, Virginia Institute of Marine Science, Gloucester Point, Virginia.

Pilings supporting the VIMS Ferry Pier exhibit a population of intertidal oysters distinctly zoned around the mean tidal level; oysters are not well distributed outside this zone. Field experiments utilizing hatchery-reared larvae were conducted in order to evaluate the relative importance of settlement versus recruitment in the establishment of the observed populations. The settlement distribution was measured with intertidally situated, Mylar-lined PVC tubes in which larvae were interned. After a designated time period, the Mylar lining was removed and the number of post-set per tidal height determined. Recruitment patterns were evaluated at five tidal heights with the aid of image analysis techniques. Larvae were allowed to settle on ceramic plates which were then photographed to record the initial number and size of the new recruits. The plates were placed in the field and photosampled weekly: a digital image processor was used to determine mortality and growth.

Both physical and biological factors were implicated as contributing to the distribution of settlement and the pattern of recruitment; the type and severity of these factors were dependent on tidal level and time. The establishment of the wild populations thus appears to be a synergistic process in which the settlement pattern is refined by post-settlement mortality. Environmental conditions, which are temporally variable, seem especially important in influencing settlement and culling new recruits.

INHIBITING FIRST POLAR BODY FORMATION IN *CRASSOSTREA GIGAS* PRODUCES TETRAPLOIDS, NOT MEIOTIC I TRIPLOIDS. L. B. Stephens and **S. L. Downing,** School of Fisheries, WH-10, University of Washington, Seattle, Washington.

At 18°C, development in the maturing eggs was sufficiently slow to separate the two meiotic divisions. Treating newly fertilized eggs with cytochalasin B from 15–30 min. after insemination, inhibited principally first polar body formation. Treatment from 40–55 min. after insemination chiefly inhibited second polar formation. Egg samples were taken from these two groups as well as from an 18°C control every 10 min. from insemination up to 120 min. These were preserved in Carnoy's solution until they were processed. At that time, samples were observed under a fluorescent microscope by air drying the eggs on a slide, and adding the dye DAPI (1 ug/ml of PBS).

In the control group, the first polar body was fully formed at 40 min., the second at 50 minutes, and first cleavage occurred at 100 min. The two polar bodies were distinct fluorescently because the first is diploid and therefore is larger and brighter than the second which is haploid. In the early treatment group, few polar bodies were observed until 50 minutes, and at first cleavage, if there was still only one polar body, its low fluorescence suggested it was haploid. Furtehrmore, in some eggs, 40 sets of chromosomes could be counted which indicated that the zygotes were tetraploid. In the late treatment group, most samples only exhib-

ited the first polar body at 40 min. In addition, we were able occasionally to count 30 sets of chromosomes confirming this group contained triploids.

The above three groups and other early treatment groups were reared in the hatchery under normal conditions except that only a small 44 micron screen was used throughout, to retain even the smallest larvae. Thousands of larvae on days 1, 2, 5, 8, 9, 10, 12, and 15 were placed in test tubes and run collectively through the flow cytometer. Results confirmed that on day 1, the early treatment group was 9% diploid and 91% tetraploid while the late treatment group was 8% diploid, 75% triploid, and 17% tetraploid. However, the 91% tetraploid percentage decreased slowly to approximately 50% on days 8 or 9, and then between the 10th and 12th day samples, the tetraploid peak almost completely disappeared (<5%). Observations under the light microscope revealed many abnormal larvae which were assumed to be the tetraploids because they also disappeared at this time. The most common abnormality was shell deformation: many larvae did not have two complete shells and thus were forced to swim constantly. No tetraploid spat have been diagnosed at this time.

IDENTIFICATION OF SOLUBLE MICROBIAL PRODUCTS THAT INDUCE SETTLEMENT BEHAVIOR IN OYSTER LARVAE (*CRASSOSTREA* SPP.). **Marianne Walch,** Center of Marine Biotechnology, 600 E. Lombard St., Baltimore, Maryland, and Department of Microbiology, University of Maryland, College Park, Maryland; **Levent Dagasan,** Department of Microbiology, University of Maryland, College Park, Maryland; **Steven L. Coon,** Department of Zoology, University of Maryland, College Park, Maryland; **Ronald M. Weiner,** Center of Marine Biotechnology, 600 E. Lombard St., Baltimore, Maryland, and Department of Microbiology, University of Maryland, College Park, Maryland; **Dale B. Bonar,** Center of Marine Biotechnology, 600 E. Lombard St., Baltimore, Maryland, and Department of Microbiology, University of Maryland, College Park, Maryland; **Rita R. Colwell,** Center of Marine Biotechnology, 600 E. Lombard St., Baltimore, Maryland, and Department of Microbiology, University of Maryland, College Park, Maryland.

Surface films of specific marine bacteria have been found to enhance settlement and metamorphosis of competent larvae of the oysters *Crassostrea gigas* and *C. virginica*. Products of one particular bacterium, *Alteromonas colwelliana,* are especially active in inducing spat set. This organism produces a set of soluble metabolites which trigger a "search" behavior that immediately precedes larval settlement. Laboratory and field experiments have shown that treatment of competent oyster larvae with these microbial products for a length of time sufficient to elicit maximal search behavior increases spat set.

Separation and identification of the soluble metabolites of *A. colwelliana* that induce search behavior has revealed at least two different kinds of active compounds. One is ammonia, a product of amino acid degradation. The other is a group of closely related products of the enzyme tyrosinase, which includes L-dihydroxyphenylalanine (L-DOPA) and one or more trihydroxyphenylalanines. The two classes of compounds appear to cue larval behavior via different cellular mechanisms. A model of how these microbial cues may operate in the natural environment has been developed, and its implications for setting of oysters in hatcheries are discussed.

THE LOCATION AND TOPOGRAPHY OF OYSTER REEFS IN THE RAPPAHANNOCK RIVER ESTUARY, VIRGINIA. **James P. Whitcomb,** and **Dexter S. Haven,** Virginia Institute of Marine Science, School of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Public oyster grounds in the Rappahannock River, VA were charted in 1976 and 1977 using an electronic positioning system to locate oysters, shell, sand or mud. Hydraulically operated patent tongs were used to sample the bottoms to validate the charts. During this study, 17277.6 ha of public bottoms were surveyed; of this total, 3845.3 ha was oyster reef, sand-shell or mud-shell bottoms; the remainder, 13432.3 ha (78%) was sand, mud or buried shell. The location, extent, topography and environment of the oyster producing areas are discussed. Setting of oysters, physiography, and productivity were analyzed.

CALORESPIROMETRY, A METHOD FOR EXAMINING RESPONSE OF OYSTER LARVAE TO HYPOXIA AND ANOXIA. **John Widdows,** Plymouth Marine Laboratory, Plymouth, United Kingdom; **Roger Mann,** Virginia Institute of Marine Science, Gloucester Point, Virginia; **Roger I. E. Newell,** University of Maryland, Horn Point Environmental Laboratories, Cambridge, Maryland.

During activity, animals produce heat. Calorespirometry allows simultaneous measurement of heat production and oxygen consumption, and, therefore, estimation of the relative contributions of aerobic and anaerobic processes to total heat production. We describe the response of veliger (90–133 μm length) and pediveliger (>260 μm length) larvae to anoxia and hypoxia in terms of heat production, oxygen consumption, feeding activity, and swimming behaviour. All larvae have anaerobic pathways and limited capability to withstand anoxia. With increasing size, anoxia tolerance increases mainly due to an ability to decrease heat dissipation and conserve energy expenditure. This is reflected in short term maintenance of high feeding and swimming in smaller larvae versus depressed but subsequently maintained rates of heat production, oxygen consumption, feeding and swimming in pediveliger larvae. We suggest that decreased activity in pediveliger larvae reflects decreased oxygen supply to the tissues associated with decreasing surface: volume ratio and that energy conserved by reducing digestion and absorption of food can largely account for the observed reduction in metabolic rate during hypoxia.

HUMAN INFLUENCES ON THE DISPERSAL OF LIVING ORGANISMS AND GENETIC MATERIAL INTO AQUATIC ECOSYSTEMS

PART I: IMPACTS/RISK ASSESSMENT

CHANGES IN THE SEA: THE MECHANISMS OF DISPERSAL OF MARINE AND AQUATIC ORGANISMS BY HUMAN AGENCY. James T. Carlton, Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon.

Human influences on the rearrangement of the aboriginal distributions of marine and aquatic (freshwater) animals and plants have been far more pervasive than anecdotal qualitative lists of "famous exotics" would suggest. A review of the synanthropic dispersal systems in place for up to five centuries indicates that humans have both altered and accelerated the natural movements of perhaps thousands of species, transcending barriers (oceans and continents) that had previously created and maintained evolutionarily isolated species and populations. These dispersal systems include *ships* (most recently the release of *ballast* (not bilge) *water*), the accidental movement of *non-target species* with *commercial fishery species*, the *release of bait, aquarium, and research organisms*, and a long list of other and somewhat more subtle mechanisms. "In contrast to land and fresh waters," wrote Charles Elton in 1958 concerning biological invasions, "the sea seems still almost inviolate". It is now clear, some thirty years later, that the contrast has faded: the human role in the alteration of the species composition and of the evolutionary role of gene flow in shallow marine ecosystems has been, and is, as pervasive as on the continents.

FISH GENETIC ENGINEERING: A NOVEL APPROACH IN AQUACULTURE. T. T. Chen, Z. Y. Zhu, and **D. A. Powers,** Center of Marine Biotechnology, The University of Maryland, College Park, Maryland, and Department of Biology, The Johns Hopkins University, Baltimore, Maryland; **R. Dunham,** Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama.

With the world population increase in recent years, there is an urgent need to increase protein production. Aquaculture and mariculture possess the greatest potential for the production of animal proteins. Recent advances in recombinant DNA technology and genetic engineering promise to revolutionize aquaculture and mariculture through manipulation of growth hormone (GH) and growth factor genes. Many laboratories, including our own, are directing research effort toward these ends. Recently, we cloned cDNA and genomic genes of GH from several commercially important fish species. These cDNAs have been expressed in *E. coli*, and the biologically active recombinant GH polypeptides have been purified. Treatment of fish with the biosynthetic GH resulted in marked increases in specific growth rates. These results open the possibility of using biosynthetic GH to promote rapid growth of cultured fish.

An alternative application of GH genes in aquaculture is the development of transgenic fish with enhanced growth rates by gene transfer technology. Through microinjection, we have succeeded in transferring trout GH cDNA fused with LTR of RSV into carp. Some progeny derived from the crosses between the transgenic males and non-transgenic females were also found to carry the trout GH cDNA. Although there was considerable variation in the sizes of the transgenic fish, they appeared to be 20% larger, on the average, than their sibling controls. Though there is evidence that transgenic fish can be constructed, the establishment of fast growing transgenic fish for aquaculture purposes still requires major research efforts.

ENGINEERING MARINE MICROORGANISMS FOR BIODEGRADATION AND WASTE CONTROL IN THE SEA. Rita R. Colwell, Maryland Biotechnology Institute, University of Maryland, College Park, Maryland.

Recent developments in genetic engineering and biotechnology have opened up new opportunities for waste control and toxic waste degradation *in situ*. Specific considerations are necessary for use of engineered organisms in marine systems, since fresh water microorganisms do not function optimally in marine systems. Marine bacteria have been employed for treatment of oil spills occurring in coastal and ocean waters with reasonable success. Isolation of oil-degrading microorganisms has been effective and can be accomplished with relative ease. New approaches have been taken to amplify and enhance strain capability for biodegradation of hydrocarbons, employing the techniques of genetic engineering. Successes to date have been good. Furthermore, marine bacteria have been isolated which are capable of degrading a variety of toxic chemicals. The genetics of these organisms is being studied, and engineering organisms for rapid clean-up of toxic chemical spills in the marine environment now appears possible.

An important factor to consider in developing marine bacteria for environmental application is that those bacteria which occur naturally at the site to be remediated should be selected as candidate strains for genetic engineering. By employing autochthonous organisms and amplifying their genes for degradative pathways or by insertion of genes coding for degradation of specific chemicals and using the techniques of genetic engineering, it should be possible to enhance *in situ* degradation and accomplish bioremediation. A useful hypothesis to test is that, upon depletion of the toxic chemical "nutrient," the engineered organism will resume occupancy of its appropriate ecological niche. Microcosms have been employed showing that, indeed, such is the case. Mesocosm studies would be useful to gather additional data prior to application in the natural environment. The potential of biotechnology, applied to marine and fresh water systems for bioremediation, waste control, and targeted biodegradation is significant. However, careful microcosm and mesocosm testing, as well as ample containment trials should be done, before large scale field application can be done.

MICROBIAL PEST CONTROL AGENTS. John A. Couch, E.P.A. Gulf Breeze Laboratory, Sabin Island, Gulf Breeze, Florida.

The majority of microbial pest control agents (MPCA's) under development are naturally occurring insect pathogens isolated from insect hosts for study and development. They include viruses, bacteria, fungi, and protozoa. More recently, the ability to genetically alter some of these microbial agents to enhance their insecticidal qualities has become apparent. Potential risks to non-target species following release of MPCA's (either natural or genetically altered) into aquatic habitats have been studied at several levels. The possible effects endpoints examined to date for non-target species include:

1. infectivity,
2. pathogenicity, and
3. toxicity.

Non-target species studied have been submergent plants, crustacea, molluscs, and fishes. Crustacea are particularly important because of their phylogenetic proximity to insects and because both Crustacea and Insecta share microbial parasites and pathogens from common taxonomic groups (genera, families, order, and classes). Examples of these studies will be described.

DISPERSAL OF EXOTIC SPECIES FOR AQUACULTURE PURPOSES: FRESHWATER SPECIES. Walter R. Courtenay, Jr., Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida.

Since the beginning of translocations of aquatic species beyond their historical ranges, there have been escapes and releases from culture facilities. Most escapes have resulted from carelessness in construction and operation of these facilities. In some instances, there appear to have been deliberate releases of stocks. To date, aquarium fish culture facilities have been the source of more introductions than has the culture of fishes for food or other purposes; future development of aquaculture of food resources, however, promises to become a greater source of introductions unless precautions are taken early.

Recognition that introduced exotic aquatic species have been, or have potential to be, detrimental to native species and ecosystems, and that they can also result in negative economic impacts is reason for concern and caution. Guidelines for importation and culture security practices must be developed that will enhance the future of aquaculture and provide protection for irreplaceable natural resources.

DISPERSAL OF EXOTIC AQUATIC ANIMALS FOR AQUACULTURAL PURPOSES WITH SPECIAL EMPHASIS ON THE HAWAII EXPERIENCE. Jack R. Davidson and **Robert W. Brick,** Sea Grant College Program, University of Hawaii, Honolulu, Hawaii.

Dispersal of exotic marine animals in the United States has occurred over a long period of time and for a wide variety of reasons. Until the mid-1960's such importation and dispersal occurred largely at the whims of state and federal government agencies and private interests. Since that time, several important legislative measures have encouraged the culture of aquatic animals and dispersal of species showing economic potential.

The Sea Grant legislation in 1966, a program with a specific mandate to encourage wide spread development of commercial aquaculture through universally-based programs of applied research and extension services was of particular significance in this regard. In addition, the missions of traditional government agencies were expanded to include aquaculture. For example, the National Marine Fisheries Services (formerly the Bureau of Commercial Fisheries) was given an aquaculture mission starting in the early 1970's. During this period the Department of Agriculture also began to expand its traditional research role to include aquatic animals beginning with catfish. Tax structures of the period encouraged private investment in aquaculture.

This awareness of and interest in the potential economic opportunities in aquaculture coincided with the development of widespread environmental awareness in the United States. With the rapidly accumulating scientific evidence that certain past introductions of plants and animals into new areas had resulted in ecological damage, the importation of aquatic animals which could purposely or inadvertently be released into streams or marine areas began to come under severe scrutiny.

The paper will examine experience with the effects of major introductions of aquatic animals for aquaculture purposes in the U.S., with special emphasis on the Hawaii experience. Hawaii offers a model worthy of study both with respect to experience with early imports of exotic aquatic animals, some of which inad-

vertently have had major impacts on marine and other aquatic ecosystems, and from the standpoint of moving relatively quickly to devise a method to screen and to control the introduction of such animals. Control of the introduction of plants and animal species into Hawaii is much simpler than other states, with the possible exception of Alaska, due to the relatively large distance from other land masses. In addition, early experience with controls to guard against the possibility of introduction of rabies and agricultural pests into the islands provided experience and a quarantine system which could be adapted to the needs to control the introduction of plant and animal species for other purposes.

MASS MORTALITIES AND INFECTIOUS LETHAL DISEASES IN BIVALVE MOLLUSKS AND ASSOCIATIONS WITH GEOGRAPHIC TRANSFERS OF POPULATIONS. **C. Austin Farley,** National Marine Fisheries Service, Maryland Department of Natural Resources Cooperative Laboratory, Oxford, Maryland.

Disease problems of oysters have been documented since the early 1920's when mass mortalities struck populations of *Ostrea edulis* in the United Kingdom. In 1926, mortalities were seen in *Saccostrea commercialis* in Australia and in *Crassostrea virginica* in Malpeque Bay, Canada, in the 1930's. Etiologic agents were not seen by the original investigators; however, epizootiological evidence implied strongly that an infectious process was operating (a parasite, *Microcytos roughleyi* has recently been described from affected Australian oysters). Microbial pathogens have been implicated in most of the more recent mortalities. *Perkinsus marinus* was described by J. G. Mackin in the 1940's as the causative pathogen in Gulf of Mexico mortalities. Epizootics of this disease were later described from the middle and southern Atlantic regions by Andrews and in oysters from Hawaii by Kern. *Haplosporidium nelsoni* (MSX) was discovered by Haskin, Mackin and Stauber in association with severe mortalities in Delaware Bay that began in 1957 and continue to the present. This disease quickly spread to Chesapeake Bay in 1959 and eventually to other Atlantic coast sites as far north as Maine and as far south as Georgia. Resistance has developed to a marked extent in progeny of Malpeque Bay disease survivors and to a limited extent in progeny of MSX survivors. A second Haplosporidan disease caused by *H. costale* was described by Wood and Andrews in oysters from Chincoteague Bay and other high salinity sites in the northeast. This disease was transferred by introduction to California waters. A disease characterized by the presence of tissue abscesses and mortality appeared in *Crassostrea gigas* in Denman Island, British Columbia, Canada in 1960 and was subsequently found by Kern in *C. gigas* from Hawaii. The causative agent was recently described as *Microcytos mackini*. Similar organisms were found in the early 1960's in 3 separate mortality episodes involving *O. edulis* that originated from the hatchery at Milford, Connecticut. This latter disease (recently identifed as *Bonamia ostreae*) transferred *en mass* to Elkorn Slough in Calfornia and was later transferred to France where it caused severe mortality in the native flat oysters. It has recently re-appeared (after transfer from the California site) in Puget Sound, Washington oysters. This problem in France was preceded by two other diseases. *Crassostrea angulata* began dying in 1965 due to iridovirus infections in the gill. This was thought to have originated from small-scale introductions of *C. gigas*. Large scale introductions of *C. gigas* to supplant the losses in the native *C. angulata* were followed by the appearance of a new fatal disease on the flat oyster caused by *Martelia refrengens*. This disease virtually destroyed the industry within 3 years of its appearance. In 1969, new mortalities occured in *S. commercialis* in Australia that were found to be caused by a closely related organism (*Martelia sidney*). Sarcoma epizootics have been seen in *O. lurida* and *Mytilus edulis* in Oregon and *M. edulis* in British Columbia where they are causing serious mortalities. An epizootic carcinoma was discovered in *Macoma balthica* in Chesapeake Bay. Etiology is not known for these neoplastic diseases. An infectious sarcoma struck *Mya arenaria* populations in New England in the early 1970's and has recently spread to Chesapeake Bay populations, causing extensive mortalities. This disease has been experimentally transmitted and transplanted and its lethality documented. It is presumably caused by a virus which is yet to be characterized.

GEOGRAPHIC DISPERSION OF THE VIRUSES IHHN, MBV AND HPV AS A CONSEQUENCE OF TRANSFERS AND INTRODUCTIONS OF PENAEID SHRIMP TO NEW REGIONS FOR AQUACULTURE PURPOSES. D. V. Lightner, R. M. Redman, T. A. Bell, and **R. B. Thurman,** Environmental Research Laboratory, University of Arizona, 2601 East Airport Drive, Tucson, Arizona.

Introductions of penaeid shrimp for aquaculture purposes from remote areas to Hawaii, Mexico, Ecuador, Brazil, and North America have documented that certain shrimp pathogens, most notably the viruses IHHN, MBV and HPV, can readily be transported with live shipments of shrimp. In some cases, these introductions have resulted in catastrophic disease losses to facilities which had imported the contaminated stocks. In others, the effects were moderate or insignificant.

Some important examples include the introduction of two virus-caused diseases, IHHN and MBV, which were discovered initially in populations of penaeid shrimp imported for aquaculture purposes into University of Arizona-operated shrimp culture facilities in Hawaii and Mexico. MBV was first recognized and described in a population of *P. monodon* that was imported from Taiwan into Puerto Penasco, Mexico in 1976. Later, MBV was found in populations of *P. monodon* imported into Hawaii from Taiwan, Tahiti, and the Philippines. Likewsie, IHHN virus was discovered in a number of populations of *P. stylirostris* and *P. vannamei* imported into Hawaii in 1980–1982 from shrimp hat-

cheries in Florida, Panama, Costa Rica, Ecuador, and Tahiti. IHHN was found in Hawaii to be a highly lethal disease of juvenile *P. stylirostris*, frequently resulting in mortality rates approaching 90% in populations reared in high density systems. Two populations of imported *P. vannamei* (from hatcheries in Costa Rica and Ecuador) were shown to carry IHHN asymptomatically, and to readily transmit the disease to previously unexposed *P. stylirostris* populations.

HPV and MBV have been found recently in several North and South America shrimp culture facilities, in shrimp imported from various Asian locations. *P. vannamei* reared at the same facilities were found to become infected by both of these viruses. While in neither case were the infections accompanied by significant disease, careless introductions such as these, and other as yet unrecognized pathogens, may result ultimately in the introduction of other devastating diseases, such as IHHN has been to *P. stylirostris*.

DISPERSAL OF MARINE PLANTS FOR AQUACULTURAL PURPOSES. Michael Neushul, Charles D. Amsler, Daniel C. Reed and **Raymond J. Lewis,** Department of Biological Sciences, University of California, Santa Barbara, California.

The great voyages of botanical exploration of the 17th and 18th centuries began to show that the macroalgal floras of the world are strikingly different. Once these floras were described, it was possible to study the effects of accidental and/or intentional introduction of "foreign" plant species. The accidental introduction of the Japanese kelp, *Laminaria japonica* to the northern coast of China, and its subsequent domestication and transplantation, now provide the basis for the world's largest plant maricultural program. In contrast, *Sargassum muticum* from Japan has been unintentionally introduced to the Pacific Coast of North America and Europe, where it is an unwelcome addition to the flora. The giant kelp *Macrocystis* has become established, after introduction, in China. Other introduced marine plants include the tropical carrageenophyte, *Eucheuma*, and the Japanese sea-vegetable, *Porphyra*. Newly developed methods now make it possible to measure algal spore longevity and dispersal. It is possible that macroalgal crop plants could be genetically modified to produce defective spores. Plants of this sort could be safely introduced, since they would not be self-propagating.

DISPERSAL OF MICROBIAL PATHOGENS THROUGH INTRODUCTIONS AND TRANSFER OF FINFISH. J. S. Rohovec and **J. L. Fryer,** Department of Microbiology, Oregon State University, Corvallis, Oregon.

Fish are transferred from one geographical area to another for many reasons. These transfers may be over relatively short distances or may span continents. Recently there have been increasing efforts to ensure that with the transfer of fish there is not a concomitant dispersal of microbial pathogens. Prior to these efforts, and in some cases in spite of them, fish pathogens have been introduced with the movement of their hosts. Protozoan, bacterial, and viral pathogens all have been disseminated with the movement of fish stocks. *Myxobolus* (*Myxosoma*) *cerebralis*, which is endemic in Europe, was transferred to a limited number of areas in the eastern United States and has been subsequently disseminated throughout most areas where salmonids are reared within the USA. *Renibacterium salmoninarum* is present in South America as a result of the introduction of salmonids into that continent. Infectious hematopoietic necrosis virus now occurs in Europe, Japan, and Taiwan as a result of fish shipments from the northwestern North America.

DISTRIBUTION OF MICROBIAL AGENTS IN MARINE ECOSYSTEMS AS A CONSEQUENCE OF SEWAGE DISPOSAL PRACTICES. Thomas K. Sawyer, Rescon Association, Inc., Royal Oak, Maryland, and Foundation for Advanced Research in Medical Sciences, Easton, Maryland.

Microbial agents present in water and sediment are reliable indicators of sewage contamination in coastal and offshore marine waters. Certain viruses, bacteria, fungi, and protozoans commonly present in sewage wastes survive in seawater for variable periods of time and are useful for monitoring both short-term and long-term changes in the environment. Fecal coliform bacteria are useful indicators of recent sewage contamination while spore-forming *Clostridium perfringens* serves as an indicator for both recent and long-term contamination. Viruses belonging to the polio, echo, and cocksackie groups are routinely cultured from sewage-contaminated bottom sediments far from shore. Attenuated strains of polio virus used for immunizations are especially useful for identifying point sources of sewage waste. Terrestrial fungi and slime molds that produce highly resistant spores have received less attention than bacteria and viruses but are known to survive in sewage-contaminated sediments. Recent studies on potentially-pathogenic free-living soil and freshwater amoebae have shown that several species of *Acanthamoeba*, associated with fatal meningitis and eye disease in humans, are commonly recovered from contaminated sediments. The amoebae form highly resistant cysts that survive changes in temperature, moisture, and salinity. Statistical analyses of data obtained from studies on microbial pathogens recovered near sewage outfalls and from ocean disposal sites provide a valid basis for following the progressive deterioration or recovery of marine ecosystems impacted by sludge contamination.

Sewage wastes are known to be a rich source of nutrients for both plants and animals. Further studies are needed to estimate the role of sludge disposal on the unchecked growth of bacteria, fungi, and protozoans responsible for diseases of marine plants, fish, and shellfish.

ENVIRONMENTAL IMPACTS OF INBRED, HYBRID, AND POLYPLOID AQUATIC SPECIES. **Gary H. Thorgaard,** Department of Zoology and Program in Genetics and Cell Biology, Washington State University, Pullman, Washington; **Standish K. Allen, Jr.,** Shellfish Research Laboratory, Rutgers University, P.O. Box 687, Port Norris, New Jersey.

The recent application of techniques for producing inbred and polyploid fish and shellfish and the use of hybrids in aquaculture and fishery management programs has led to increased concern about the environmental impacts of such forms. These manipulated forms represent a special case of the general problem of environmental impacts of organisms that have been genetically manipulated by conventional or non-conventional means. Genetically altered organisms may harm natural populations of species by competing with, interbreeding with, or replacing them.

Sterile organisms are least likely to have negative impacts on natural populations. Sterile hybrids or triploids thus seem least likely to have harmful effects when introduced because their genetic impact on natural stocks should be minimal or minimized. However, sterile hybrids or triploids might in some cases interfere with reproduction of natural stocks in non-gentic (e.g., behavioral) ways.

Fertile hybrids have sometimes had very negative impacts on natural populations and should not be used outside closed systems. Fertile hybrids may, however, provide an opportunity for introducing beneficial genes or chromosome segments into domesticated stocks. Inbred strains have not been widely used in aquaculture or fishery management but would be expected to have negative effects if interbreeding led to decreased genetic diversity.

HUMAN INFUENCES ON THE DISPERSAL OF LIVING ORGANISMS AND GENETIC MATERIAL INTO AQUATIC ECOSYSTEMS

PART II: MANAGEMENT/RISK REDUCTION AND SAFETY

CALIFORNIA'S APPROACH TO RISK REDUCTION IN THE INTRODUCTION OF EXOTIC SPECIES. **Robson A. Collins,** California Department of Fish and Game, Marine Aquaculture Coordinator, Sacramento, California.

Calfornia now takes a conservative approach to the introduction of new species to its lands and waters. Although we have had some notable successes with the introduction of exotic species, the introduction of others, both with official permission and without, has resulted in problems that are still prevalent today. California is especially concerned with the possible introduction of disease organisms to already existing populations, and with the displacement of native species by introduced species.

CANADIAN STRATEGIES FOR RISK REDUCTION IN INTRODUCTIONS AND TRANSFERS OF MARINE AND ANADROMOUS SPECIES. **Roy Drinnan,** Department of Fisheries and Oceans, Box 550, Halifax, Nova Scotia, Canada.

Canada with a huge land mass, extreme climatic variation, commercial fishery activity on three oceans, and a growing aquaculture industry presents a diversity of risks associated with introductions or transfers:

1. Introduction or spread of pest organisms or diseases,
2. Genetic impacts from stocks transferred within the species range,
3. Negative ecological impacts of introduced species by direct competition, etc.

'Introduction' includes imports to the country and internal transfers between geographically and biologically separated areas, and both native and exotic species. The unit control area varies with the perceived risk. This is basically, for constitutional and administrative reasons, a province; for more subtle effects, and given sufficient knowledge, smaller discernible systems and biological sub-units, watersheds, etc. represent the unit control area.

Control is effected by mandatory government approval of virtually all introductions and transfers to a province, or smaller areas. For salmonids, national legislation specifies requirements for approval. For other species, regional authorities, operating within broad guidelines, assess risk and potential impact and, where approval is granted, specify procedures and requirements, including holding in or breeding from quarantine, monitoring of biological parameters, and criteria for release.

EFFECTIVE APPLICATION OF AQUACULTURE DISEASE CONTROL REGULATIONS—RECOMMENDATIONS FROM AN INDUSTRY VIEWPOINT. **Ralph Elston,** Battelle Marine Research Laboratory, 439 West Sequim Bay Road, Sequim, Washington.

Transportation of aquatic animals for commodity distribution,

research purposes by the general public, and for aquatic animal husbandry purposes is inevitable within North America and between continents, to a lesser degree. Historical analysis demonstrates that introduced pathogens can have catastrophic results. Although the risk is not necessarily proportional to the quantity and frequency of movement of a given species, it is likely to increase with the diversity of species movements. As a sophisticated aquaculture industry continues to expand, it is vital to realistically address the problem and solutions.

Risk from aquatic animal movements can be reduced but not eliminated. Past failures have resulted from the lack of information transfer and lack of recognition of the significance of infectious diseases, such as in the case of the introduction of the oyster pathogen, *Bonamia ostreae*, to Europe. Thus, in addition to a more complete inventory of infectious diseases of marine organisms, effective transfer of data to resource management agencies and the effective utilization of this technology is needed today. In addition, the scientific community interested in this subject needs to develop an objective means of classifying the potential significance of infectious organisms. For example, too little substantive information is available on the numerical impact of diseases on natural or husbanded populations of animals. As well, certain categories of infectious agents, e.g. viruses, are typically regarded as highly significant, de facto, without consideration of their potential for pathogenicity.

In the application of effective disease control in an age of incomplete technology, it is particularly important to recognize that philosophy usually overrides technology. Thus it is incumbent on resource managers charged with controlling animal diseases to adopt reasoned and workable policies. These cannot be zero-risk policies. Failure of policies has often resulted from an overzealous attempt to control animal movements and the failure to recognize the multiple avenues of animal movements as well as from the lack of implementation of animal movement controls. One important need in the control of exotic animal diseases is the education of the aquaculture industry concerning the risks of introduction of exotic pathogens. In addition, resource managers need to address the other potential avenues of pathogen transfer which include processed commodity distribution, research programs, and movement by the general public.

A FRAMEWORK FOR MANAGING THE RISKS OF DELIBERATE RELEASES OF GENETIC MATERIAL INTO AQUATIC ECOSYSTEMS. Dr. Robin S. Gregory, Associate Program Director, Decision, Risk, and Management Science, National Science Foundation, Washington, D.C.

Releases of genetically-altered organisms into the environment constitute a concern because of their potential for adverse consequences to human health and the natural environment. Recent surveys have shown that the public believes genetic engineering will create social benefits but also will lead to costs, including risks to human health and ecosystems, of unknown severity. Because the public's understanding of the consequences of new technologies generally is based on partial and at times misleading information, the framework by which risk/benefit tradeoffs are evaluated is likely to be incomplete. Thus, there is a need for a rational, consistent program to assess the risks of genetic releases to the aquatic environment and to structure a meaningful dialogue with the public about this information.

Risk assessments focusing on the expected physical damages of technologies have become commonplace, and much of this structure may be relevant for assessments of deliberate genetic releases to aquatic ecosystems. However, this transfer is likely to be only partial, for several reasons. First, both dispersal and exposure models for genetically-altered aquatic organisms are likely to be highly uncertain because of the abbreviated track record of genetic manipulation. This creates serious problems, both in terms of how the analysis is done (e.g., the assessment of cumulative impacts) and in terms of how information is communicated (e.g., problems of unintentional bias). Second, technologies that are new and perceived to present possibly catastrophic consequences tend to be highly dreaded by large segments of the public. This has important implications for the conduct of a risk assessment (e.g., in terms of the choice of stakeholder groups and the types of tradeoffs likely to be considered). Third, risk management policies that encompass low-probability, high-consequence events need to combine assessments of potential physical damage with psychological and sociological considerations. Yet analysts have little experience with such frameworks, particularly in cases where the benefits are likely to be highly uncertain as well.

This paper will examine these questions from the perspective of a potential regulator, emphasizing the use of risk assessments in developing a rational decision-making framework for evaluating the net social benefits of deliberate releases of genetic material to the aquatic environment.

SHELLFISH HEALTH AND PROTECTION. F. G. Kern, National Marine Fisheries Service, Oxford Laboratory, Oxford, Maryland; **A. Rosenfield,** Center for Environmental & Estuarine Studies, University of Maryland, Cambridge, Maryland.

The role of humans in the dispersal and enhancement of aquatic animal pathogens, pests, predators, and competitors that may adversely affect the productivity and quality of our living marine resources is of particular concern to fishery biologists and resource managers. More recent concerns involve the accidental or deliberate introduction into marine ecosystems of exotic and genetically manipulated species of micro- and macroorganisms. Some introductions have proved beneficial, but others have caused significantly harmful effects on resident biota and/or their habitats.

The above concerns as well as the origins (sources) of "biological pollution" of marine ecosystems will be discussed, with spe-

cial reference to the need for developing risk assessment and risk management strategies. Other discussion points will include federal-state interactions regarding shellfish transports between U.S. coasts, territories, and individual states.

GUIDELINES FOR INTRODUCING AQUATIC ORGANISMS: VOLUNTARY OR MANDATORY? Christopher C. Kohler, Fisheries Research Laboratory, Southern Illinois University, Carbondale, Illinois.

The American Fisheries Society (AFS) has taken a leadership role on the global issue of fish introductions dating back to 1969. A formal "Position of the American Fisheries Society on Introductions of Exotic Aquatic Species" was endorsed by the membership in 1972. The AFS Exotic Fish Section was formed in 1980 and has initiated a number of activities addressing exotic fish issues. The section name was changed to be the Introduced Fish Section in 1985 to broaden its scope to include transplanted species. The section, upon the request of the AFS Environmental Concerns Committee, updated the AFS position statement which was subsequently published and adopted in 1986. Voluntary compliance with the intent of the position statement within the aquaculture industry is recommended. Non-compliance could lead to legislation being enacted that would not provide the same flexibility in imports/exports currently being enjoyed by the industry.

NATIONAL BIOSAFETY PROGRAMS FOR FIELD TESTING TRANSGENIC ORGANISMS. D. R. Mackenzie, National Biological Impact Assessment Program, Cooperative State Research Service, USDA, Aerospace Bldg., Washington, D.C.

Traditionally, agricultural research progresses from basic investigations in laboratories to field tests in plots, paddocks or ponds to verify the intended improvements under realistic conditions before commercial use. This sequence applies to conventional research as well as biotechnology.

Several Federal agencies have regulatory authority and/or program responsibilities to provide proper safeguards for experiments or commercial uses of transgenic organisms. It is now generally accepted that adequately contained laboratory experiments with transgenic organisms offer little or no threat to the environment or public health. Field testing does present additional biosafety questions that have now been addressed at the Federal level.

Currently, Federal biosafety programs are based on the premise that the *products* of biotechnology are not fundamentally different from the products of conventional research. Consequently, virtually no new regulations have been enacted specifically for biotechnology products. Thus, the products of biotechnology are to be regulated only insofar as they would be regulated articles anyway.

The biotechnology research *process* will continue to be reviewed under voluntary guidelines that spell out safe practices for agricultural experiments with biotechnologically transformed organisms. This biosafety oversight will continue to be conducted primarily at NIH for contained laboratory experiments and, more recently, at U.S.D.A. for confined field tests. U.S.D.A. also requries permits for field experiments.

Both types of biosafety assurances (regulations and guidelines) rely on available knowledge and/or scientific advisory committee judgments as a part of the review process. To develop needed biosafety knowledge, as well as undergird this system, the U.S.D.A./CSRS has established the National Biological Impact Assessment Program (NBIAP) to facilitate safe field testing by providing:

1. Information system support,
2. Monitoring networks,
3. Research initiatives aimed at developing needed protocols, methods and practices for safe field tests with biotechnologically transformed organisms.

(Details of the NBIAP will be presented and discussed.)

INTRODUCED ORGANISM: POLICIES AND ACTIVITIES OF U.S. FISH AND WILDLIFE SERVICE. James A. McCann, U.S. Fish and Wildlife Service, Gainesville, Florida; **Robert A. Peoples, Jr.,** and **Lynn B. Starnes,** U.S. Fish and Wildlife Service, Washington, D.C.

Until recently, U.S. Fish and Wildlife Service efforts regarding introduced species problems and issues have been limited to three areas. The first is a regulatory process based on authority in the Lacey Act that allows the Service to prohibit the import of species found to be injurious. However, Service regulations (50 CFR 16) cover only a limited number of species, and the species included have not been significantly expanded since those regulations were first adopted in 1974. In addition, the Service along with all other Federal agencies must abide by the provisions of the Presidential Executive Order on Exotic Organisms (E.O. 11987) that prohibit the introduction or export of exotic organisms by Federal agencies or federally funded or permitted activities. The Service has adopted as its policy the draft regulations that were developed to implement the Executive Order which was proposed in 1977, but never finalized.

In line with its third area of effort, the Service recently established a Center in Gainesville, Florida, to track the exotic fish already established in the Nation's open waters (43 species) or likely to become introduced in the near future. The Center supports federal, state, and local efforts to stop further introduction of harmful species and to evaluate and promote those species with beneficial characteristics which can be manipulated in such a way as to not threaten the environment.

Based on extensive review of this issue over the past 2 years, the Service has decided to assume a more aggressive role in furthering efforts to address and resolve introduced species concerns. This will involve some unilateral actions such as a restatement of

Service policy consistent with the current understanding of the issue and listing additional species such as the mitten crab in its Injurious Wildlife Regulations. However, the focus of this Service initiative will be to work with all affected parties to establish national and international policies and programs for dealing with this problem on a continuing basis.

STATUS OF UJNR POLICY ON THE INTRODUCTION OF EXOTIC SPECIES FOR AQUACULTURE. James P. McVey, NOAA National Sea Grant College Program, Washington Science Center, Rockville, Maryland.

The United States Japanese Natural Resources Panel on Aquaculture (UJNR) consists of scientists from both countries who are interested in the exchange of information on the developing field of aquaculture. Meetings are held once a year on an alternating basis in each country to discuss new developments in aquaculture and opportunities for cooperation between the two countries. Topics for discussion are chosen well in advance and leading scientists from each country are asked to give presentations on their areas of expertise within the topic.

There has been a long-standing concern and discussion on the hazards and opportunities associated with the use of exotic species in aquaculture for both countries. The UJNR is now in the process of developing a set of recommendations on the policies that should be adopted for the use of exotics in aquaculture. This policy will more than likely be dependent on the final Federal position of all the agencies involved in aquaculture development and regulation for both countries.

The U.S. agencies that are reponsible for aquaculture are developing a coordinated policy, through the Joint Subcommittee on Aquaculture, which will clarify the U.S. Federal policy in this area. Once this is done the UJNR will finalize its recommendations in line with this and the existing Japanese policies on the use of exotics in aquaculture.

MODEL SEAFOOD SURVEILLANCE PROGRAM. G. Malcom Meaburn, National Marine Fisheries Service, P.O. Box 12607, Charleston, South Carolina; **E. Spencer Garrett,** NOAA, NMFS, National Seafood Quality and Inspection Laboratory, Pascagoula, Mississippi.

The Model Seafood Surveillance Program (MSSP) study was authorized by Congress in the 1987 fiscal year budget to have NOAA design "a program of certification and surveillance to improve the inspection of fish and seafood consistent with the Hazard Analysis Critical Control Point system." The National Marine Fisheries Service is proceeding with the study utilizing a three-pronged approach: product safety, plant hygiene, and economic fraud. The product safety issue will be addressed through a contract to the National Academy of Science. Plant hygiene, and economic fraud issues will be addressed using the Hazard Analysis Critical Control Point (HACCP) concept during specific industry by industry workshops conducted in conjunction with National Fisheries Institute and other trade associations through Saltonstall/Kennedy grants. The final product which NOAA intends to deliver to Congress will be a surveillance system for seafood products which provides for reasonable consumer protection in the consumption of fishery products, and treats imported, domestic, and exported products equably. A description of the background, approach, and progress to date of the study will be given.

ECONOMIC PRESSURES DRIVING GENETIC CHANGES IN FISH. Nick C. Parker, U.S. Fish and Wildlife Service, Southeastern Fish Cultural Laboratory, Rt. 3, Box 86, Marion, Alabama.

The demands for fish and fishery products in this country and throughout the world are expected to continue to expand faster than the supply. From 1982 through projections for 1988, the global supply of fish increased 11% while the volume traded among 162 nations increased 16%. Imports of fish and fishery products in the United States were valued at $365 million in 1960 and $8.8 billion in 1987, when the imports consisted of $3.1 billion worth of nonedibles and $5.7 billion for edible products. Excluding manufactured goods, the trade deficit for fish and fishery products ($7.1 billion) in 1987 was second only to petroleum and petroleum products ($16.2 billion). By comparison, the top five agricultural products imported, listed by actual value and as a percent of the total deficit, were vegetables and fruits $4.3 billion, 2.5%; coffee $2.8 billion, 1.6%; crude rubber $1.2 billion, 0.7%; cocoa $1.1 billion, 0.6%; and sugar $0.4 billion, 0.2%. The annual per capita consumption of fish in the U.S. increased over 20% from 1975 to 1987 when it reached 7.0 kg. It is expected to be 13.6 kg by the year 2020. The world's catch of fish from the ocean was 90 million metric tons in 1986, up from 57 million metric tons in 1966, and the maximum sustainable yield is projected to be 100–120 million metric tons.

In 1987, more than 11% of global landings were produced by aquaculture. Production of farm-raised aquaculture species is forecast to be 22 million metric tons, about 25% of the world's harvest, by the year 2000. The demand for sport fish is expected to increase as rapidly as the demand for food fish. In 1985, 58 million anglers in the United States spent $28.2 billion in 987 million angler days. Some public waters in several states are now managed as put-and-take fisheries and in some areas as catch-and-release fisheries. How will resource managers meet the demands of the public as fishing pressure increases? Already some anglers have paid $900/day to fish for 3-kg trophy-size bass in private waters. The catch of channel catfish from fee-fishing operations frequently resembles a supermarket activity, and over 500 kg/day of fish have been taken by anglers from a 0.1-ha pond. There exists a strong and growing economic basis to produce genetically altered fish to improve growth rate, disease resistance, food conversion, thermal tolerance, lipid content, age of maturity, and

sporting qualities of game fish. Almost assuredly aquatic resource managers, aquaculturists, anglers, and investors will continue to produce new hybrids, transgenetic species, and polyploids. Both native and non-native species will become increasingly important as a source of genetic material to propogate specialty fish for recreation, food, bait, and to control aquatic vegetation.

ROLE OF THE INTERNATIONAL COUNCIL FOR THE EXPLORATION OF THE SEA (ICES) IN MATTERS CONCERNED WITH TRANSFERS AND INTRODUCTIONS OF MARINE ORGANISMS. Carl J. Sindermann, Oxford Laboratory, Oxford, Maryland.

The North Atlantic nations, functioning through the International Council for the Exploration of the Sea, have made good progress during the past 15 years in drawing attention to problems associated with transfers and introductions of marine species, and have developed a basic code of practice which member countries have endorsed. A critical ingredient of the code is a recommendation that only F_1 individuals derived from quarantined adults should be introduced, and not the adults themselves. Original concern about introductions of exotic pathogens has been augmented in recent years by concerns about ecological disturbances and genetic modifications. Because of the virtual irreversibility of successful introductions to marine waters, the problem is particularly acute, and calls for concerted international response.

Some of the ICES objectives include effective communication at appropriate levels, adoption of codes of uniform practices (insofar as national capabilities permit), and attempts at international uniformity in inspections and regulations. Proposed strategies to reduce risks from deliberate introductions include the development of governmental awareness of the potential effects of such actions, the establishment of regional and even international committees to discuss problems related to introductions and to develop mutually acceptable procedures, and the inclusion of considerations of introductions on the agendas of international regulatory bodies concerned with living resources.

CRUSTACEAN AND BIVALVE BIOLOGY AND CULTURE

EVIDENCE OF A SEMIANNUAL REPRODUCTIVE CYCLE FOR THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS* (GMELIN), IN THE MID-ATLANTIC REGION. William D. DuPaul, James E. Kirkley, and **Anne C. Schmitzer,** Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia.

The reproductive cycle of the sea scallop , *Placopecten magellanicus* in the mid-Atlantic region was studied over a 15-month period. One to fifteen samples a month were collected from commercial vessels fishing from Long Island to Cape Hatteras in water depths of 37–68 m. A gonadal index was calculated for five shell size intervals as an indicator of the reproductive cycle. A sharp decline in mean gonadal indices between April and May 1987 and a subsequent increase and decrease in indices between September and November 1987 indicated reproductive processes were occurring on a semiannual cycle. A major spring spawning season was reconfirmed in 1988 by a rapid increase in mean gonadal indices between December 1987–January 1988, followed by variable declines in the indices through June. The occurrence of spawning activity for two consecutive spring seasons in addition to a fall spawning season suggests that a semiannual reproductive cycle may be a characteristic feature of *P. magellanicus* in the mid-Atlantic region. The ramifications of spring spawning to the mid-Atlantic sea scallop fishery and management policies are addressed.

NONPLANKTONIC DEVELOPMENT OF THE PERICALYMMA LARVA OF *SOLEMYA VELUM* (BIVALVIA: SOLEMYIDAE) Richard G. Gustafson and **Richard A. Lutz,** Rutgers Shellfish Research Laboratory, Rutgers University, New Brunswick, New Jersey.

The veiled awning clam *Solemya velum* Say, known to possess sulfide-oxidizing bacterial symbionts in its gill, inhabits coastal waters from Nova Scotia to northern Florida at depths of 0–12 m. Four spontaneous spawning events of adult *S. velum* occurred in the laboratory. Subsequent developmental stages were observed with light and electron microscopy. Cultures were maintained at 18–19°C and salinities varied little from 32‰. Embryonic and pericalymma larval stages, typical of protobranch bivalves, develop within individual adhesive gelatinous capsules and offspring emerge at hatching as benthic juveniles. Fertilized eggs are light orange in color, spherical and have an average yolk-mass diameter of 193.8 μm (±5.3 μm, n = 12). The overall egg capsule diameter is about 525 μm. Entirely ciliated cylindrical pericalymma larvae (318.3 ± 20.3 μm in length by 208.8 ± 16.2 μm in cross-sectional diameter, n = 25) are obtained within 24 h. These larvae lack an apical ciliary tuft, possess seven rows of calymma or test cells and are very active within the capsule, rotating counterclockwise about the long axis of the body when viewed from the anterior. During metamorphosis, which occurs within 48 h of fertilization, the calymma or larval ectoderm is entirely ingested. The prodissonconch measures 319.8 ± 14.3 μm in length by 215.4 ± 8.1 μm in height (n = 25). The foot and ciliated gill buds are well developed by 72 h after fertilization and subsequent growth contributes to the dissoconch or adult shell. Hatching begins 13 days after fertilization when at least three gill filaments have formed on either side of the mantle cavity and the shell measures 402.3 ± 18.4 μm in length by 251.4 ± 14.3 μm in height (n = 25). All growth and development to this point occur at the expense of yolk reserves. Actively crawling and burrowing juveniles were cultured in the presence of 0.1 mM sodium sulfide. Due to the adhesive nature of the gelatinous capsule, the larval dispersal capability of this species is estimated to be on the order of only a few meters.

FEEDING ECOLOGY OF *CALLINECTES SAPIDUS* IN CHESAPEAKE BAY—IMPLICATIONS FOR SOFT-SEDIMENT MARINE BENTHIC PREDATOR-PREY DYNAMICS. R. A. Mansour and **R. N. Lipcius,** Virginia Institute of Marine Science, Gloucester Point, Virginia.

Two key componets of predation, i.e., the functional response (where predators increase prey consumption as prey abundance increases) and the aggregative response (where predators congregate in areas of high prey density) may be density-dependent and vary as a function of environmental features. However, few studies have addressed the interactive effects of these components upon predator–prey dynamics.

We are investigating:

1. Interference and the functional and aggregative responses of the blue crab, *Callinectes sapidus* Rathbun, to soft-shell clams, *Mya arenaria* Linne, in the laboratory,
2. The natural diet of three size classes of male and female blue crabs collected from three subestuaries of the Chesapeake Bay—the York, Rappahanock and James Rivers, Virginia.

The results and implications of these studies will be discussed.

UNRAVELLING A COMPLEX INTEROCEANIC DISPERSAL HISTORY OF THE BIVALVE *MACOMA BALTHICA*. **Brian W. Meehan,** Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia; **James T. Carlton,** Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon.

The tellinid bivalve *Macoma balthica* (L.) has an extensive geographic range that reaches from temperate to arctic coastal waters in both the North Atlantic and North Pacific oceans. Recent studies have indicated that eastern and western North Atlantic populations are morphologically and genetically different from one another, and that they may have diverged as sibling species. To determine the genetic relationship between *M. balthica* from the Pacific and Atlantic coasts of North America, populations from each coast were examined at eleven enzyme loci using standard starch gel electrophoresis. Allele frequency data indicate that *M. balthica* populations from San Francisco Bay, California are more closely related to western North Atlantic populations and that *M. balthica* populations from Oregon are more closely related to eastern North Atlantic populations. We suggest that San Francisco Bay populations were introduced relatively recently from western North Atlantic populations. The Oregon populations are probably a natural extension of northern populations that extend along Northern Asia to the eastern North Atlantic. The results of additional genetic comparisons using mtDNA restriction fragment analysis that are currently being conducted will also be presented.

EVIDENCE OF FEEDING SELECTIVITY AND A FEEDING SELECTIVITY THRESHOLD IN THE MUSSEL (*MYTILUS EDULIS*) FED ON NATURAL PARTICLE ASSEMBLAGES. **Carter R. Newell,** Great Eastern Mussel Farms, Tenants Harbor, Maine; **Sandra E. Shumway,** Maine Department of Marine Resources, West Boothbay Harbor, Maine; **Terry L. Cucci,** Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine.

Particle selection, both as a function of size and organic content, by the mussel, *Mytilus edulis*, was investigated using flow cytometric techniques. Feeding of mussels from several discrete locations was monitored using natural particle assemblages from the respective areas as food sources. Cells were analyzed for differences in their fluorescing intensities as well as particle size (spherical diameter) and samples were preserved for bacterial counts. Results indicated:

1. Prefiltering of samples reduced the microscopic cell counts by as much as 75% and much less when smaller diatoms were dominant,
2. The presence of long-chain phytoplankton species resulted in an underestimation of cell number when counted on the flow cytometer,
3. Clearance rates by mussels were approximately 40% higher on chlorophyll cells than on non-chlorophyll cells on 5 of the 6 days sampled. There was evidence on day 6 that high levels of non-chlorophyll particles inhibited the ability of mussels to feed selectively.

Results are compared to water samples taken directly above a commercial lease site in which food quality was lower directly over the mussel bed than that measured higher in the water column. The implications of a feeding selectivity threshold on mussel energy acquisition are discussed.

AQUACULTURE FEASIBILITY OF THE AUSTRALIAN MARRON LOBSTER, *CHERAX TENUIMANUS* (CRUSTACEA: DECAPODA: PARASTACIDAE) IN THE U.S. **David B. Rouse** and **Izuddin Kartamulia,** Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama, **Noel C. Alon, Michael C. Rubino** and **Charles A. Wilson,** Bluewaters, Inc., 4350 East–West Highway, Suite 600, Bethesda, Maryland.

As part of a continuing research and development program to determine the feasibility of culturing the marron lobster (*Cherax tenuimanus*) in the U.S., an outdoor culture study with juvenile marron was conducted. Growth and survival were evaluated at three densities in outdoor tanks. Juvenile marron (mean size = 1 g) were shipped from Western Australia and acclimated for 3 weeks in indoor fiberglass troughs before stocking. Densities of 4, 8 and 12 juveniles/m^2 were stocked in nine, 20-m^2 rectangular concrete tanks at the Auburn University Fisheries Experiment Station. Salt was added to the aerated culture water to maintain a 150–250 ppm NaCl concentration. A 40%-protein commercial shrimp diet and additional habitats were provided to optimize growing conditions.

Despite seemingly optimal water quality conditions, marron survival after 3 months varied considerably from 0 to 71%, without apparent density effects. Most mortalities occurred during a high temperature (27–30°C) period. Cumulative growth rates ranged from 0.24–0.52 g/week (mean = 0.34 g/week) with no significant density effects. These results indicate that marron culture can be feasible in the U.S. under certain specific conditions which are discussed.

FOOD VALUE OF TROPICAL MICROALGAE TO BIVALVE LARVAE. **Antonieto Tan Tiu** and **David E. Vaughan,** Division of Applied Biology, Harbor Branch Oceanographic Institution, Inc., 5600 Old Dixie Highway, Fort Pierce, Florida.

Microalgae (Solar Energy Research Institute collection) were

grown at 30°C in 30o/oo salinity seawater that was enriched with modified Guillard nutriments, while feeding experiments were done at 30°C and 25o/oo salinity. Fifteen combinations of four microalgae, namely, *Chaetoceros muelleri* Lemmermann (Chaet14), *Ellipsoidon* sp. (Ellip1), *Isochrysis* aff. *galbana* Green (T-iso) and *Nannochloris* sp. (Nanno2) were fed to bivalve larvae of *Crassostrea virginica* (Gmelin 1791), *Cyrtopleura costata* (Linne 1758) and *Mercenaria mercenaria* (Linne 1758) to determine their food value through larval development. Based on enhanced growth, survival and metamorphosis in larvae of *C. virginica, C. costata* and *M. mercenaria,* the best diet consisted of equal proportions of Chaet14, Ellip1 and T-iso. Quantity of the different amino acids in diets consisting of different combinations of microalgae is more stable than in single microalga, and seems associated with the results of feeding experiments.

EFFECTS OF INORGANIC AND ORGANIC NUTRIENT ENRICHMENT ON GROWTH AND BIOENERGETICS OF THE BLUE MUSSEL, *MYTILUS EDULIS*. Gregory A. Tracey, Science Applications International Corporation, c/o U.S. Environmental Protection Agency, Narragansett, Rhode Island.

The effects of inorganic and organic enrichment on growth and bioenergetics of the blue mussel, *Mytilus edulis,* were experimentally tested using outdoor, 13-m^3 experimental marine ecosystems (mesocosms). Matching additions of nutrients or sewage sludge over an 8-fold concentration range provided the potential for differing environmental conditions of water quality, food availability and food quality that might occur in marine waters receiving anthropogenic wastes. Growth of mussels (shell length, dry tissue weight) within mesocosms declined with increased loading from both nutrient sources. Effects due to reduced water quality (metals, hydrocarbons, pH, hypoxia, ammonia toxicity) were discounted. Chlorophyll *a* (chl *a*) concentration was the best predictor of growth (r^2 = 0.98), despite being a variable and often minor component of the seston. Physiological mechanisms for maintenance of food-proportional growth were investigated via mussel exposures to mesocosm waters of controlled suspended particulate concentration. Gross growth efficiencies (dry weight gained/food absorbed) at equivalent food concentrations were reduced in treatments of increasing enrichment, indicating reduced food quality. Differences in food quality were attributed to food "dilution" effects (e.g., chl *a*/TSM ratio). In apparent response to reduced food quality, ingestion rates at equivalent food concentrations increased with increasing enrichment, thus counteracting food dilution effects. These results suggest that *M. edulis* can maintain food-proportional growth in environments widely varying in water and food quality.

REPRODUCTION OF THREE GENERATIONS OF GRASS SHRIMP (*PALAEMONETES PUGIO*) IN THE LABORATORY UNDER CONSTANT CONDITIONS. William F. Van Heukelem and **Ronald D. Anderson,** University of Maryland, Center for Environmental and Estuarine Studies, Horn Point Environmental Laboratories, Cambridge, Maryland.

Larvae of *Palaemonetes pugio* were reared to adulthood in the laboratory in a closed system in "Hughes larval tanks". Larvae, juveniles, and adults were fed freshly hatched *Artemia* nauplii daily. Juveniles and adults also received commercial fish food. Cultures were maintained at a salinity of 12–15‰, at a temperature of 25–28°C and a light cycle of 15L/9D. First generation females began bearing eggs at 167 days of age and by 24 months of age they had spawned eleven times. Second generation cultures began bearing eggs at only 81 days of age and third generation shrimp first bore eggs at 77 days. Spawning occurred throughout the year under the constant environmental conditions maintained in the laboratory whereas spawning in the field occurred only from May through August. Laboratory reared females did not grow as large as those in the field and hatched fewer larvae per brood. Only 28% of first generation shrimp and 31% of second generation shrimp were females.

WEST COAST MOLLUSCAN AQUACULTURE

A SAND SUBSTRATE NURSERY FOR GEODUCK CLAMS (*PANOPE ABRUPTA*). J. Harold Beattie, Washington State Department of Fisheries, Point Whitney Shellfish Laboratory, 1000 Point Whitney Road, Brinnon, Washington.

The Washington State Department of Fisheries has been working with the hatchery and nursery culture of geoduck clams (*Panope abrupta*) since the early 1970's. A need for artificial supplementation of geoduck stocks became obvious in the mid-1970's when surveys of commercially harvested subtidal beds indicated low levels of recruitment. Initial use of upwells proved largely unsuccessful as a geoduck nursery. Implementation of sand substrate nurseries has resulted in an increase in annual production from a few thousand to nearly 10 million geoduck seed.

Presently we are using two configurations of nurseries: 2 circular tanks, 3 m (10 ft.) in diameter, and 8 rectangular raceways, 3.3 × 6.1 m (11 × 20 ft.). Each nursery contains a sandwich of pea gravel on the bottom, a water permeable industrial polyester fabric in the middle, and sand on top. We add newly metamorphosed geoducks to the sand layer. Survival to planting size ranges between 6–10%, resulting in a final density of about 50,000 animals per sq. m. Mean growth approximates 0.1 mm shell length per day.

Our total system requires only 6–10 man-hours per week. An upwell system for an equivalent amount of animals would require up to 88 upwells and about 14.6 man-hours per day. Sand substrate nurseries may lend themselves to the successful and cost-efficient culture through the juvenile phase of other molluscs and are especially applicable where labor is at a premium.

THE POTENTIAL OF THE JAPANESE SCALLOP, *PATINOPECTEN YESSOENSIS*, FOR WEST COAST AQUACULTURE: GROWTH AND SURVIVAL OF JUVENILES IN BRITISH COLUMBIA WATERS. N. Bourne, Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada; **C. A. Hodgson,** Ministry of Agriculture and Fisheries, Aquaculture and Commercial Fisheries, Pacific Biological Station, Nanaimo, British Columbia, Canada; **W. Carolsfeld,** Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada.

As part of ongoing scallop culture research at the Pacific Biological Station, Nanaimo, British Columbia, several native and imported species have been investigated for ease of culture and suitability for British Columbia waters. Of the species examined, *Patinopecten yessoensis* has shown the most promise.

Japanese scallops reared at the Pacific Biological Station (F1 generation) were set out at 8 sites along the B.C. coast to examine growth and survival of juveniles in hanging culture. One year old animals (approx. 2.0 cm shell height) were set out at the sites between April and May 1987. Animals were placed in hanging culture nets suspended at 5, 10, and 15 m from the surface and were monitored over a 12-month period.

Of the 8 sites, growth and survival of scallops at 3 sites were good during the first 5 months of the study. Survival ranged between 96–100%, and growth rates were 0.249–0.304 mm/day. Scallops held at 15 m at the 3 sites had marginally slower growth rates than scallops held at other depths. Growth and survival for the remaining 7-month period of the study differed significantly between site and depth. Growth rates ranged between 0.140–0.236 mm/day. Maximum average size attained was 10.2 cm and the best survival for the 12-month period was 96%.

At the remaining 5 sites, growth and survival were poor and in some cases no animals survived for the 12-month period. Physical deterioration of many of the animals was believed to be stress-related and may have been caused by local site conditions or susceptibility to movement of the hanging culture system used. A second growout study is planned for 1989 and will attempt to find correlations between physical characteristics of a site and growth and survival.

POTENTIAL FOR CLAM CULTURE IN BRITISH COLUMBIA, CANADA. Rick M. Harbo, Fisheries and Oceans, 3225 Stephenson Point Road, British Columbia, Canada; **Neil Bourne,** Pacific Biological Station, Nanaimo, British Columbia, Canada.

The potential for culture is great in British Columbia with its extensive shoreline and protected waters. Waters are nutrient rich, temperate, and relatively pollution free. The species with the highest potential and market demand is the manila clam, *Tapes philippinarum*. Manila clam culture will be initially limited to the south coast for biological and economical reasons, problems with PSP, remoteness from markets, and unfavourable growing conditions. Because natural clam beds are currently being protected to support the wild fishery, efforts need to be directed to enhancing and protecting less than ideal culture ground. Options include improving the bottom by spreading gravel, and the control or removal of predators. There are not any areas known where natural clam seed can be collected in any great quantities. Hatchery seed must be planted and protected to prevent loss from wave action and predation. The optimum levels of seeding, advantages to using larger seed and enhancing and protecting growing area need to be assessed before clam culture will be economically attractive.

CHALLENGES AND OPPORTUNITIES IN ALASKA SHELLFISH MARICULTURE. William Michael Kaill, Division of Fisheries Rehabilitation, Enhancement and Development, Alaska Department of Fish and Game, Box 3-2000, Juneau, Alaska.

There are some factors favoring shellfish mariculture in Alaska: physical opportunity (a long and complex coastline), relatively high water quality, productive waters, and local communities having favorable attitude. Challenges are institutional (permitting, tidelands leasing), site selection (suitable temperature and productivity can be narrowly site-specific), seed supply (must be affordable, reliable, consistent), PSP and other contamination, and economics (logistics, scale of operation, market).

Although the potential is great, Alaska's mariculture industry has not really begun in an industrial sense. There are research projects and small or start-up operators in Alaska that can illustrate some of the ways that these promises and challenges have been dealt with.

PHYSIOLOGICAL ENERGETICS OF JAPANESE SCALLOP LARVAE. Bruce A. MacDonald, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.

Techniques of physiological energetics were used to assess energy requirements of Japanese scallop larvae to help determine optimal conditions for rearing this species in a hatchery environment. Growth and ingestion rates were determined for *Patinopecten yessoensis* larvae reared at temperatures between 10–18°C and fed various concentrations of Tahitian *Isochrysis*. Larvae were held in experimental chambers at densities of 0.5–100 per ml to assess the influence of crowding on growth, respiration and feeding rates.

Short term feeding studies suggested that ingestion rates could remain constant at larval densities between 1–5 per ml provided that food levels were increased accordingly, However, longterm growth studies revealed slower growth and reduced survivorship if larvae were reared at densities exceeding 2 larvae per ml. High respiratory demand and comparatively slow growth rates for this species were reflected in lower growth efficiencies than those previously reported for bivalve larvae. These scallop larvae appar-

ently require a minimum food concentration of 7–15 cells per µl (depending on size) to gain sufficient energy to support respiration and growth. Information from this study and those on mussel and oyster larvae indicate that despite morphological similarities between species of bivalve larvae they may differ greatly in their rates of energy acquisition and utilization.

ABALONE NUTRITION AND THE POTENTIAL ROLE OF PURIFIED DIETS, Karen Norman-Boudreau, Shellfresh International, 2610 Meier Rd., Sebastopol, California.

Abalone aquaculture has greatly expanded in the United States over the recent years. This industry's growth is now currently limited by the availability of natural feeds both in terms of location and amounts available. Abalone nutritional understanding is limited but enough is known to construct a purified diet for abalone to use in place of natural feeds (macroalgaes). Reported feed conversion ratios on natural diets are very high. Artificial feeds are in use in Japan but are cost prohibitive for use in the United States (about $3.50/kg).

Preliminary prototype diets have been constructed and accepted by abalone in pilot trials. Early growth tests on these purified diets are encouraging. Further testing and validation of growth rates on proposed abalone diets will enable this industry to grow and expand in locations where natural feeds are not available. Nutritional findings for abalone will have potential application in other molluscan culture situations.

PROVEN TECHNOLOGY NOW AVAILABLE FOR EFFICIENT COMMERCIAL ABALONE PRODUCTION. F. R. Oakes, The Abalone Farm, Inc., Cayucos, California.

Hatchery technology for the efficient production of juvenile abalone has been demonstrated by many producers, including companies operating in the United States and Canada. Existing hatchery producers now offer abalone seed for sale to prospective growers. Further development of the abalone culture industry, however, has been greatly hindered by the lack of proven technology for on-shore growout of abalone seed to marketable size. The Abalone Farm, Inc. (AFI) has pioneered on-shore growout and now offers a profitable alternative to the traditional in-ocean growout technology developed by other producers in California and Japan. The AFI system utilizes a modified raceway tank design to achieve a low cost growing environment capable of supporting densities up to 1.25 lbs./gallon. The growout system is easily transferable to other coastal production sites. The system technology can be acquired through joint venture with full technical support supplied by AFI. System components can also be acquired from conventional equipment manufacturers for aquaculturists who do not require technical assistance. With proven technology now available for profitable abalone growout, existing marine aquaculturists have an easy opportunity to diversify their production. New aquaculture producers also have a greater opportunity to enter the business without extended periods in research and development.

EFFECT OF DIETARY ALGAL CONSTITUENTS ON THE TISSUE COMPOSITION AND ENERGY IN THE LARVAE OF THE SCALLOP *P. YESSOENSIS*. John N. C. Whyte and **Norma G. Ginther,** Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada.

The objective of this study was to correlate the nutritional condition of premetamorphic scallop larvae with the content of macronutrients in mixed algal diets supplied. Three diets, a binary diet of *Isochrysis* aff. *galbana* and *Chaetoceros calcitrans* and two ternary diets composed of the binary diet with added *Tetraselmis suecica* and with added *Thalassiosira pseudonana*, were fed to the larvae. Biochemical analysis of the diets and the larvae showed that the diets with the highest levels of lipid or protein did not produce the most energetically favoured larvae. The ternary diet with *T. pseudonana* containing the highest level of carbohydrate, mainly glucan, provided the larvae with the highest nutritional condition and demonstrated the significant role played by carbohydrate in balancing nutrient uptake. The binary diet provided lipid with the highest content of docosahexaenoic acid, whereas lipid in the ternary diet with *T. pseudonana* contained the highest level of eicosapentaenoic acid. These acids, considered nutritionally essential, were incorporated into larval tissue dependent on their relative abundance in the diets.

WATER QUALITY AND TOXINS

PARALYTIC SHELLFISH TOXINS: PRODUCTION, DETECTION AND THERAPY. John A. Benson, Edward C. Braden and **Michael Neushul,** Neushul Mariculture Inc., 475 Kellogg Way, Goleta, California.

Toxin-producing algae are found world-wide, in both fresh and marine waters. The toxins produced by these plants are of interest to neurophysiologists, toxicologists, mariculturalists and biologists seeking to understand the adaptive value of these substances to the organisms that produce them. There is a current need for toxin standards, definition of the source organisms, methods for detection and quantification of the toxins, and therapies for persons having consumed the toxins.

Four known dinoflagellate strains in the *Gonyaulax/Protogonyaulax* group have been cultivated and the toxins extracted from them. Differences in the toxin profiles were quantified using HPLC, and compared to total toxicity determined using the new fly bioassay. Growth rate and toxin profiles of *Protogonyaulax tamarensis* strain 545 were compared for plants grown in different dilutions of F/2 culture media; peak growth rate was measured in F/8 media. No evidence was found for conversion of the toxins by *Mytilus edulis* fed *P. tamarensis* strain 545. In order to develop a

therapeutic strategy, monoclonal antibodies to saxitoxin have been developed. At the time of this writing these are being characterized.

THE WATER QUALITY OF COASTAL SHELLFISH GROWING AREAS: THE SHELLFISH HARVESTER'S TROUBLED PAST & UNCERTAIN FUTURE. Jeffrey Kassner, Town of Brookhaven, Division of Environmental Protection, 3233 Route 112, Medford, New York.

Harvesting shellfish from the coastal waters of the United States is a socially and economically important, as well as a traditional, industry. While shellfish harvesters must confront many occupational problems and uncertainties, shellfish growing area water quality related issues are perhaps the most serious. Water quality issues have had negative direct and indirect impacts upon harvesters and have the potential to profoundly change the way in which the shellfish industry operates. New York is a major shellfish producing state and its case history typifies the consequences of water quality upon shellfish harvesters.

New York has approximately one million acres of marine waters and in 1986, over 1200 shellfish harvesters, known locally as baymen, landed hard clams, oysters and soft clams valued at over $12.7 million. Due to both point and non-point source discharges, nearly 19% of New York's waters, some of which are very productive, are closed to shellfishing for failure to meet water quality standards. This has resulted in the extinction of several local shellfisheries and has concentrated harvesting in open areas, contributing to the potential for overfishing. Periodic media reports of illness attributed to the consumption of shellfish and marine environmental quality problems have caused demand for shellfish to drop temporarily, causing baymen to lose income. Regulating and patrolling closed shellfishing areas has diverted effort from shellfish conservation activities, potentially lowering long term resource productivity.

Water quality issues present baymen with an uncertain future. Further declines in water quality will place more acreage off limits. Changes in the standard or regulations could have the same result, alter the way in which baymen operate, for example, by mandating depuration, or divert additional state resources from management. Additional reports of shellfish attributed illnesses and marine pollution could further erode consumer confidence and baymen income.

PSP AND OTHER SHELLFISH TOXINS: RECENT OUTBREAKS AND RESEARCH. Sherwood Hall, Seafood Toxins Research Project, U.S. Food and Drug Administration, HFF-423, 200 C. Street, S.W., Washington, D.C.

Bivalves, which are otherwise wholesome and a valuable food resource, can accumulate dangerous levels of potent natural toxins. In many areas, monitoring programs exist to detect and intercept contaminated shellfish before they get to market. However, occurrences of new kinds of shellfish toxicity, or toxicity in areas not protected by monitoring programs, continue to cause difficulty. In 1987, there were outbreaks of PSP in Guatemala and NSP in North Carolina. Both are known syndromes, previously unknown in these areas. In November of 1987, an entirely new form of sehllfish toxicity occurred in Eastern Canada, apparently due to the accumulation of the neuroactive substance domoic acid. Current research at the FDA is directed towards understanding the nature and occurrence of these toxins and developing the tools to deal with them, to permit safe consumption of wholesome shellfish.

THE QUALITY OF SHELLFISH GROWING WATERS. Dorothy L. Leonard and **Marlene A. Broutman,** Strategic Assessment Branch, National Ocean Service, National Oceanic and Atmospheric Administration, Rockville, Maryland.

The Quality of Shellfish Growing Waters project examines the quality of shellfish growing waters in estuaries adjoining the Atlantic Ocean, Gulf of Mexico, and Pacific Ocean. Waters are classified as approved or harvest-limited (prohibited, conditionally-approved, restricted) for the commercial harvest of oysters, clams and mussels based upon public health concerns. State regulatory agencies classify waters based upon a shoreline survey, hydrologic studies and the monitoring of ambient water for fecal coliform levels.

The project expands upon the 1985 National Shellfish Register of Classified Estuarine Waters (Register) that summarized acreages of shellfish growing waters by classification and state. The Register data have been clarified, aggregated by estuary and related to water quality. Information is presented on the administration of state shellfish programs, status of classified waters, sources of pollution affecting harvest-limited waters, and trends in classifications between 1971–1985. Data were collected by site visits to 23 states, through interviews with state and Federal agency personnel, discussions with shellfishermen, and by reference to written materials. Data were compiled for over 100 estuaries identified in NOAA's National Estuarine Inventory.

Over one third of shellfish growing waters in the United States are closed to the harvest of molluscan shellfish at least part of the year. In some estuaries, i.e., in Louisiana, Florida and Maryland, shellfish waters are managed based upon rainfall and/or river stage. Often these conditionally-approved areas are the most productive. In the Northeast the major contributing causes for closure are the presence of wastewater treatment plants, combined sewer overflows and urban runoff. The Mid-Atlantic Region experiences impacts from marinas, wastewater treatment facilities and urban runoff. In the Southeast limiting factors are runoff from agricultural activities, wildlife and wastewater treatment plants. Gulf of Mexico shellfish waters are affected by faulty septic systems, agricultural runoff and impacts from pollution sources located upstream. The West Coast experiences problems similar to the other

regions with the addition of fecal pollution from marine mammals.

DEPURATION SYSTEM FOR MOLLUSKS IN TOMALES BAY, CALIFORNIA. Jim K. Wilson, Shellfresh, 5850 Fredericks Rd., Sebastopol, California. (Former Farm Manager, Tomales Bay Oyster Company, Tomales Bay, CA).

In an effort to reduce loss of sales caused by winter rainfall closures imposed by the State of California Department of Health Services a depuration system was designed and put into operation at the Tomales Bay Oyster Company (TBOC) in Point Reyes Station, Calfornia in the fall of 1987.

The depuration system reduces coliform counts using sand filters in conjuction with an ultraviolet-light (u.v.) system. Bay water drawn in through a 6″ intake line flows through the sand filters, through the u.v. system and on into concrete wet-storage tanks. The design criteria for the depuration system are based on its ability to purge and hold a one week supply of oysters for sale.

Conditional approval for this system has been granted by the Department of Health Services. Approval was based on a total and fecal coliform testing program implemented during the winter of 1987–1988. To meet approval guidelines, TBOC oysters must be harvested prior to rain closure periods and then held in the tanks in depuration mode. However, tests made in January of 1988 showed that meat samples from oysters harvested *during* a closure period were brought to below legal standards for coliform counts within forty-eight hours of being placed in the depuration system.

Using the depuration system within approved harvesting periods, winter rainfall closures previously accounting for a loss of up to 50 percent of TBOC's sales period should be substantially reduced.

IMPACTS FROM SEWAGE EFFLUENT ON AN OPEN OCEAN SHELLFISH FARM. Jeffrey S. Young, Pacific Seafood Industries, Inc., P.O. Box 2544, Santa Barbara, California.

The discharge of partially treated sewage effluent from sewage treatment plants (STP) into coastal waters can degrade the water quality of coastal resources. This practice adversely impacts beneficial uses, including fishing, recreation, and shellfish culture. Non-disinfected sewage effluent contains pathogenic bacteria and viruses, and bivalves growing in contiguous receiving waters potentially concentrate these organisms.

Commercial and sport-harvested shellfish used for human consumption are regulated by federal and state health institutions using fecal coliform bacteria (FC) as indicator organisms. When the level of FC in growing waters or shellfish meat exceed limits set by regulatory guidelines, the waters are closed to harvesting and the shellfish are considered unfit for human consumption. The level of FC from non-point source runoff can be correlated with rainfall and thus predicted. The levels of FC in an open ocean environment are harder to predict and to do so successfully would require continuous monitoring of oceanic conditions and STP operations.

Since 1983, Pacific Seafood Industries, Inc. has cultured European flat oysters on a state lease ¾ miles off-shore of Santa Barbara, California. Longlines are used to suspend oysters at mid-depth in a water column of 23–27 meters. From 1983–1985, water analysis demonstrated FC levels below the regulatory limit of 14 FC (MPN/100 ml). FC analysis of oyster meat tissue began in December 1985 when commercial sales began. Analysis revealed levels exceeding the market standard for oyster meat of 230 FC (MPN/100 ml). Subsequent testing of oyster meats since 1985, along with comparisons to rainfall and runoff events, indicate bacterial sources other than from non-point rainfall or runoff sources impacting off shore waters. These findings will be presented along with a discussion of how oceanographic conditions, rainfall, and STP discharges work to adversely impact an offshore shellfish farm, and how critical the need is, for more extensive monitoring of STP activities to protect the states natural resources and beneficial uses.

MUSSEL CULTURE

CRUSTACEAN PREDATION ON BIVALVE PREY: AN OVERVIEW OF INTERACTIONS FROM NORTHEAST U.S. COASTAL WATERS. P. J. Auster, National Undersea Research Program, The University of Connecticut at Avery Point, Groton, Connecticut.

Direct underwater observations of predation on bivalve prey in northeastern U.S. coastal water (<30 m depth) indicate that crustaceans were generally the major taxa contributing to mortality due to predation. Patterns of predation (behaviorally, spatially, and temporally) vary with features such as distribution of predator shelter, size class of predator and prey, and water temperature. Interactions are hierarchical in nature and exhibit stochastic patterns over short spatial and temporal scales. These observations indicate site selection and maintenance are critical to fishery enhancement and mariculture programs.

INFECTIOUS DISEASES OF MUSSELS, ESPECIALLY PERTAINING TO MUSSEL TRANSPLANTATION. Susan M. Bower, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada.

To date, epizootic diseases, like those that have devastated the oyster culture industry in some parts of the world, have not been encountered by the mussel culture industry. The apparent lack of information on diseases in mussels may be attributable to the lack of research due to the lesser economic importance of this bivalve in comparison to oysters. However, several diseases ranging from haemotopoietic neoplasia of unknown aetiology through infections with pathogenic protozoans and metazoans have been de-

scribed. Thus cultured mussels are at equal risk of experiencing high mortalities from infectious disease as other cultured marine molluscs. Mussles (*Mytilus edulis*) are also known to be suitable hosts for *Marteilia refringens*, an oyster pathogen in Europe, and thus may serve as reservoirs of infection. Unregulated transplantation of mussels not only increases the chance of introducing pathogens to naive and susceptible mussel stocks but also has the possibility of introducing pathogens to other molluscs. In either case, the consequence of an unfortunate disease introduction could be the curtailment or elimination of an existing or a potentially valuable new mollusc culture industry in any geographic area.

MUSSEL CULTURE IN THAILAND: A SYNOPSIS. **Kashane Chalermwat** and **Richard A. Lutz,** Rutgers University, Shellfish Research Laboratory, P.O. Box 687, Port Norris, New Jersey; **Piamsak Menasveta,** Sichang Marine Science Research and Training Station, Chulalongkorn University, Bangkok 10500, Thailand.

Thailand lies between latitudes 6–21° N in Southeast Asia and has a coastline of approximately 2670 km. With a production of 67,510 MT of mussels in 1986, Thailand is the second largest producer of mussels in Asia, after China. Two species of mussel are cultured, the green mussel, *Perna viridis*, and the striped horse mussel *Musculus senhauseni*. Of the two species the green mussel is more important from a commercial standpoint both in terms of production area and harvested biomass. Most mussel culture activities are confined to the Upper Gulf of Thailand provinces of Chonburi, Chachoengsao, Samut Prakarn, Samut Songkram and Petchaburi.

Before the introduction of mussel culture on bamboo poles in the late 1950's, mussels were harvested opportunistically from bamboo poles used to construct fish traps. With adoption of western fishing technology and expansion of the Thai fishing fleet into international waters, the large, relatively inefficient, bamboo fishing structures became obsolete. As fewer fish traps were built, the culture of green mussels on bamboo poles specifically designed for mussel culture became more widespread. The production of *Perna viridis* reached a peak in the early 1970's and dropped dramatically in 1972 and later years.

Production of mussels in the 1980's has steadily increased, reflecting a commitment on the part of the Royal Thai Government to both aquaculture and effective coastal management. Many international agencies have aided the Thai government in implementation of its mollusc culture programs. Beginning in December 1981 cooperative efforts between the active agencies was initiated to more effectively develop coastal aquaculture of bivalve mollsucs. Among the species given highest priority in such initiatives has been the green mussel *Perna viridis*. Studies of the economics and marketing activity associated with the culture of this species have been centered at Kasetsart University. Studies focusing on the basic biology, as well as the development of more effective production systems have been conducted at Chulalongkorn University. Modern mussel culture in Thailand is presently in the research and development stage. The development of extensive culture systems for mussels as well as other species of bivalve molluscs holds much promise for the future economic development of coastal communities.

DEVELOPMENTS IN BOTTOM CULTIVATION OF MUSSELS AND OYSTERS IN THE NETHERLANDS: STUDIES ON THE EFFECTS OF STORM SURGE BARRIER CONSTRUCTION. **Renger Dijkama,** Netherlands Institute for Fishery Investigations, P.O. 77, 4400 AB Yerseke, Netherlands.

A vast project of dam construction, dike heightening and other coastal engineering works in the low-lying southwestern part of the Netherlands has had positive as well as negative effects on molluscan shellfish cultivation in the Netherlands. The loss of many small and old-fashioned processing installations made scale enlarging possible, as well as renovation of processing procedures and an increase in quality and output of the mussel processing industry. At the same time, the sheltered environment offered by the barrier invited pilot-scale experiments with cultivation of cockles (*Cerastoderma edule*), following the same procedure as in mussel cultivation.

A negative effect of the project was that a number of fishing harbours and sites for cultivation of the blue mussel (*Mytilus edulis*) and the European flat oyster (*Ostera edulis*) had to be given up.

The construction of a flood-gate storm surge barrier caused a reduction in tidal exchange and current velocity. A research program, undertaken to assess the impact of this barrier on mussel and oyster cultivation and on the local ecosystem, indicated as positive effects locally lower current velocities, making bottom culture possible on locations where this had been impossible before. On the other hand, low current speed caused siltation and mortality on a number of cultivation plots. This year experiments have started with trial plots for mussel cultivation. Besides exploration of new sites for bottom culture, these experiments are aimed at assessing mortality and changes in biomass on the plots. Also, the role of the stock of cultivated mussels in the ecosystem is investigated, notably food consumption and recycling of suspended matter.

RAFT CULTURE OF MUSSELS IN GALICIA (SPAIN) AND FRANCE. **Antonio J. Figueras,** Instituto Investigaciones Marinas, Muelle de Bouzas s/n Vigo, Spain.

Spain is the world's largest producer of cultured mussels. Between the socio economic factors to be taken into account we can consider: the availability and low cost of labour and the almost incredible ecological factors that are achieved in the rias, that

makes the growth of mussels faster than in any place in Europe, U.S.A. and Canada. Mussel culture in Galicia is a very recent industry. It started in 1947. In Galicia the total number of rafts is around 3000 and the production is between 250,000–300,000 tons.

The rias are sunken river beds in coastal regions, deep (40 m in the ria de Vigo, 60 in the ria de Arosa) and with a muddy bottom. Among the ecological conditions that favor the growth of mussels are: the high primary production, the big amount of particulated organic matter present in the ria, the characteristic configuration of the rias that gives shelter and the adequate depths to this kind of culture, the strong tidal currents which provides a constant change of water without causing any trouble to the culture ropes or to the different steps of the culture, mild and relatively constant temperatures and high salinity that provides an ideal environment for the growth of mussels.

In France (Brittany) mussel culture is carried on bouchots, that is wooden poles that are stuck into the sand or the mud. This method is used because mussel farming is carried out on the gently sloping intertidal grounds, a zone over 1 km broad. Rows of poles serve to catch the mussel seed directly on the surface of the pole or on coco-fibre ropes that hang in between the poles. In a latter phase the seed is transferred to bouchots placed somewhat higher in the intertidal zone reserved for growth and fattening. With a simple funnel placed on a stand, cylindrical nylon nets are filled with mussels, producing "boudins" (blood sausages) of 5 m in length with a diameter of about 10 cm. Two nets will be attached to each pole, one at the top end, the other somewhat lower. In the case of spat that has been caught with ropes, these ropes are wrapped directly around the pole. Mussel culture is carried out also at the Etang de Thau in the Mediterranean coast. The total production is about 45,000 tons.

PARASITES AND DISEASES OF MUSSELS. Antonio J. Figueras, Instituto de Investigaciones Marinas, Muelle de Bouzas s/n Sapin.

The lack of bibliography about the diseases and parasites of the mussel does not mean a better health situation than other molluscs but a less economic importance if we compare it with the oyster. There are few references in the literature about mortalities in mussels. The more important ones are the ones documented but not explained by Korringa in Dutch waters in the 40's, 50's, the one in Prince Edward Island in 1977 described by Li and in Italy (Munford et al. 1981). The first destroyed the Dutch mussel industry, and *Mytilicola intestinalis* was blamed.

Organisms belonging to almost all the groups that have parasites of molluscs have been detected in the two "species" of mussels. The goal of this paper is to review the literature adding data that have been obtained in a recent study on histopathology of mussels of the east coast of the United States and from Galicia in Spain.

A MODEL OF CARRYING CAPACITY FOR SUSPENDED MUSSEL CULTURE IN EASTERN CANADA. J. Grant and **K. R. Thompson,** Department at Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada.

Rapid growth of mussel (*Mytilus edulis*) aquaculture in the Maritimes has placed increasing demands on resources in coastal waters. As culture sites expand, overstocking of mussels results in reduced growth rates, and less market product. Although studies of bivalve feeding indicate that advection of suspended food is a limiting resource under these conditions, the role of water flow in supplying organic particles to cultured bivalves is poorly known.

We propose to model carrying capacity of coastal sites for suspended mussel culture and determine criteria for site selection, stocking density, and number of leases, based on estimated production potential. Our model consists of a numerical physical submodel of tidally- and wind-forced circulation, a particle submodel of measured and predicted seston fluxes, and a mussel submodel of ingestion, assimilation and respiration. Detailed field measurements of current and particle fields (Ship Harbour, Nova Scotia and regional literature data will be used to derive empirical relationships for boundary conditions, and test submodel predictions. Model output, verified by field growth trials, will predict growth of mussels at a given density and location within the harbour and hypothetical manipulation of lease area, lease number, and location. Assessment of carrying capacity will lead to efficient use of finite lease space, optimize mussel growth rates, permit financial planning through projected yields, and allow informed regulation of inshore waters for aquaculture and competing interests such as traditional fisheries.

RECRUITMENT AND COMMERCIAL SEED PROCUREMENT OF THE BLUE MUSSEL *MYTILUS EDULIS* L. IN MAINE. Herbert Hidu, Bernard McAlice, and **Linda Kindlom,** Ira C. Darling Center, University of Maine, Walpole, Maine; **Carter Newell,** Great Eastern Mussel Farms, Tenants Harbor, Maine; **Greg Podniesinski,** Normandeau Associates, 25 Nashua Road, Bedford, New Hampshire.

A thorough understanding of the processes of recruitment in the blue mussel is necessary to allow the new industry to maximize seed procurement in a manner which does not impinge upon other fisheries. Larval occurrence is a relatively precise event in Maine, cued to attaining early summer water temperature of 10–12°C in association, apparently, with full moon spawning events. Mussel larvae are more abundant on the flood tides indicating inshore and estuarine retention. However, the flood tide enhancement depends on the morphometry and relative energy of the system. The relatively wide Webb Cove embayment with maximum sample station current velocity at 0.2 m/sec. showed a random ebb tide vs. flood tide larval distribution; the 19 km narrow "arm of the sea" Damariscotta River estuary with 0.35 m/sec. current velocity showed flood tide larval enhancement in

the X2 to X4 range; and the 3 km Jordan River with 1.5 m/sec. current velocities showed flood tide enhancement of mussel larvae and byssally drifting juveniles to X20. Thus certain Maine estuarines may act as larval traps providing areas of concentrated settlement and seed abundance. Primary (larval) setting occurs most often with a large initial pulse in June followed by one or more secondary pulses throughout the summer, whereas secondary settlement (reattachment of bysally drifting juveniles) occurs at lower levels throughout the year, especially in late July and early August. Maximum attachment of larvae and juveniles occurs during periods of maximum current velocity.

Preliminary information indicates extensive eelgrass beds at the mouths of some estuaries (i.e., Jordan River) may be the sites of extensive primary setting with the drifting juveniles then moving to secondary settlement sites. Great Eastern Mussel Farms, the industry component, guided by these studies, is experimentally deploying waste mussel shell and live mussel cultch to develop and optimize a new seed procurement system.

GROWTH, REPRODUCTION, AND LONGEVITY OF MUSSELS (*MYTILUS EDULIS*): THEIR IMPLICATIONS TO MUSSEL CULTURE. G. S. Jamieson and **G. D. Heritage,** Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada.

Mytilus edulis is a circumboreal species in the northern hemisphere, with suggested significant life history differences between stocks from the Atlantic and Pacific Oceans. Mussels from British Columbia have both higher growth and mortality rates in their first year than do mussels from Atlantic Canada. In British Columbia, in contrast to the western Atlantic, growth is substantial throughout the winter and mussels can reach the currently preferred commercial size of 50 mm shell length in 12–14 months. However, growth of 1-year-old mussels declines significantly in the summer and fall when they spawn, and after reproducing, the mortality rate of these mussels generally increases dramatically and most mussels die. Although not yet confirmed, this is hypothesized to result from a high natural predation rate of mussels in British Columbia, with resulting selection in the Pacific for a more invasive, ephemeral genotype.

This summer mortality of the adult population has had adverse effects on the development of a strong mussel culture industry in British Columbia, and the balance between reproduction, survival and growth is currently being investigated. Seed source and culture site are both major factors influencing growth and mortality, and minimizing mortality is currently the most important factor in maximizing yield. Eighteen mussel culture sites have been investigated in British Columbia to date, and some locations have significantly lower summer mortality rates than others. The implications of such population differences are discussed in both the context of mussel physiology and ecology and its long-term implications for the development of an expanded, viable mussel culture industry in British Columbia.

THE NOAA NATIONAL STATUS AND TRENDS MUSSEL WATCH PROGRAM. G. G. Lauenstein, USDC NOAA National Ocean Service Office of Oceanography and Marine Assessment, Rockville, Maryland.

The National Oceanic and Atmospheric Administration's National Status and Trends Mussel Watch Program began in the winter of 1986 with the collection of bivalve molluscs and sediments from 150 sites around the United States, including sites in Alaska and Hawaii. Analyses from the third annual cycle of this program were recently completed. Spatial and temporal trends in estuarine/coastal environmental quality will be presented showing concentrations of measured analytes on a comparative basis. Specific chemical data are for select trace elements including arsenic, cadmium, lead, mercury, and tributyl tin, and summary trace organic data for total chlorinated pesticides, total DDT, and total PCB.

SEED COLLECTION AND REPRODUCTION. A. L. Mallet, Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada.

Reliable and abundant supplies of mussel seed are an essential prerequisite for the commercial viability of a mussel industry. Although mussel settlement is both temporally and spatially variable, certain environmental conditions that seem to consistently promote high recruitment will be discussed as follows:

1. Environmental characteristics,
2. Spawning level and larval mortality, and
3. Metamorphosis and early juvenile performance.

In addition to recruitment levels, other factors may affect the overall ranking of a seed-producing site. In Atlantic Canada, early settlement is preferable since the seed size at the November harvest will be more appropriate for sleeving. Shell hardness and seed condition may affect survival during transport, handling and overwintering. The origin of the seed stock also has a major effect on growth and mortality; annual production rates among stocks at a given site can vary by as much as 300%. Obviously, the ranking of seed-producing sites is dependent on several key variables which are prioritized differently by different producers. Data on the preliminary assessment of several seed-producing sites in Atlantic Canada will be presented.

MUSSEL CULTURE IN CHINA. Winston Menzel, Department of Oceanography, Florida State University, Tallahassee, Florida.

The latest FAO statistics (1986) show that mainland China is the leading country in mussel production, surpassing that of Spain. Three species are harvested commercially, the blue mussel

Mytilus edulis, the green *Perna viridis* and the thick shell mussel *Mytilus coruscus*. The blue mussel occurs in northern China southward to the northern part of the southern Yellow Sea. The thick shell mussel is more temperate and is abundant on rocks around most of the islands of the Yellow Sea and East China Sea. The green mussel is a warm water species, occurring in the South China Sea and southern part of the East China Sea. Blue mussels are the species cultured, although some culture has been done with the green musels but is limited by danger from typhoons and serious predation. The thick shell mussel has not been cultured but has been harvested on a limited basis for centuries. Data are not available on what percentage of the harvest is from culture but the increase in production in recent years is correlated with the increase in cultured mussels.

This account is for the blue mussels *Mytilus edulis*. Culture began in the early 1970's and has extended southward to the East China Sea beyond the southern limit of the natural occurrence of this species. Seed are obtained from wild set on the longline raft culture of kelp, practiced extensively in northern China, or from cultch placed out for spat attachment. Density of spatfall has increased as much as twenty five-fold since the start of extensive culture. In addition some seed are supplied by hatcheries which started experimentally in the late 1950's. Large scale hatcheries were started in the early 1970's with improved techniques of better cultured algal food, use of cheaper antibiotics for bacterial control and better cultch material. Up to 10 million spat, size 350–400 um, have been reared per cubic m of culture water.

Floating raft culture of 50–60 m long lines, buoyed with glass floats, from which are suspended 80–120 culture ropes about 1.5 m long, placed 0.5–0.8 m apart, is the method mostly used. Each culture rope has about 1000–1500 mussels and yield at harvest about 1500 kg per long line. Seed mussels are attached to the culture ropes by several methods. Usually growing ropes with mussel attached are placed out in August–September and harvested the following March–April, size 45–55 mm. Some are left out until September–October when the mussel sizes are 70–80 mm.

AN OVERVIEW OF WORLD MUSSLE CULTURE. C. R. Newell, Great Eastern Mussel Farms, Inc., Tenants Harbor, Maine; **R. A. Lutz** and **R. G. Gustafson,** Rutgers Shellfish Research Laboratory, Rutgers University, New Brunswick, New Jersey.

Mussels, represented by a variety of species within the bivalve mollusc family Mytilidae, are cultured in both marine and estuarine environments in numerous countries throughout the world. All techniques currently utilized rely upon the gathering or natural settlement of seed mussels on various substrates. While technologies exist for the production of mussel larval and juvenile stages under controlled culture conditions, commercial hatcheries are not envisioned as contributing significantly to the total world production of mussels in the foreseeable future.

For at least the past 40 years, Europe and/or Asia have consistently been the leading regions in the world for both mussel culture and harvest. The dramatic increase in production of *Mytilus edulis* and *Mytilus galloprovincialis* since the mid-1960's is a marked reflection of increased mussel culture efforts in Spain (raft culture), France (bouchot culture), the Netherlands (bottom culture), West Germany (bottom culture), and Italy (fixed platform hanging culture). Among the Asian countries, Thailand, China, and Korea have been responsible for the vast majority of landings of *Perna viridis* (Thailand and China) and *Mytilus crassitesta* (Korea).

The production status and range of aquaculture methods utilized throughout the world will be summarized.

A CASE HISTORY OF FECAL COLIFORM CONTAMINATION IN NOVA SCOTIA. D. J. Scarratt, Department of Fisheries and Oceans, Biological Sciences Branch, P.O. Box 550, Halifax, Nova Scotia, Canada; **A. R.Menon,** Department of the Environment, Air and Water Branch, 45 Alderney Drive, Dartmouth, Nova Scotia, Canada.

Progressive environmental deterioration resulting from effluent discharges from a variety of industrial sources, as well as general run-off from a Nova Scotia coastal community, resulted in the closure of an area, which includes a mussel lease, for harvesting of shellfish. Despite clean-up efforts, water quality remains too variable to permit conditional openings. Relaying of cultivated mussels to clean areas paradoxically may increase fecal coliform counts. Arguments are presented for co-ordinating all levels of government, private sector enterprises, and individual citizens in programs aimed at resolving conflicts in coastal zone management, and stimulating opportunities for shellfish culture.

SHELLFISH HARVEST/CULTURE AND TOXIC ALGAL BLOOMS: ARE THEY MUTUALLY EXCLUSIVE? Sandra E. Shumway, S. Sherman-Caswell and **John W. Hurst,** Maine Department of Marine Resources, West Boothbay Harbor, Maine.

Toxic algal blooms occur worldwide and in some areas they are a common and seasonal occurrence. Historically, attention has been focused on blooms of toxic dinoflagellates (e.g., *Protogonyaulax tamarensis*). More recently, attention has been turned to other species (e.g., *Dinophysis, Aureococcus, Gymnodinium*). These blooms often present problems with respect to optimal utilization of the shellfish resources and the magnitude of economic losses can be catastrophic. Nevertheless, successful culture facilities and commerical harvests persist in areas prone to toxic algal blooms. In this paper we examine the means by which harvesters, managers and industry cope with the problems associated with toxic algal blooms and make recommendations for the most effi-

cient and successful utilization of resources in the face of environmental instability.

AN ECONOMIC ANALYSIS OF THE MAINE MUSSEL INDUSTRY. James Wilson and **Douglas Fleming,** Department of Economics, University of Maine, Orono, Maine.

Opposition to aquaculture development often stems from fears about competition in final markets. This paper addresses that question through an examination of the growth over the last ten years of the mussel industry (wild and cultured) in the State of Maine. The paper concludes that in this instance, the ability to hold and develop leases created a strong, and never before present, incentive to actively market mussels. This new demand had strong positive benefits for both the cultured and wild segments of the industry.

In general, the paper concludes that aquaculture is likely to be highly complementary to wild fisheries because of final market effects. The principal effects of aquaculture development will be the evening out of seasonal supplies allowing broader marketing, and upward pressure on product quality which will also enhance marketing and a reduction in price volatility, also enhancing market expansion.

POSTER SESSION

***PERKINSUS MARINUS:* TEMPORAL AND ENVIRONMENTAL ASPECTS OF INFECTION IN SOUTH CAROLINA OYSTER POPULATIONS. M. Yvonne Bobo, John J. Manzi,** and **Victor G. Burrell,** South Carolina Marine Resources Research Institute, Charleston, South Carolina.

The haplosporidian, *Perkinsus marinus,* has been responsible for significant mortalities in oysters, *Crassostrea virginica,* populations. A number of studies have demonstrated that this oyster pathogen is more prevalent under conditions of high salinity and temperature. *Perkinsus marinus* has been studied in several different geographical areas of South Carolina for approximately fifteen years. Results of these studies have shown that the parasite was ubiquitous throughout the study period and at all salinities sampled (7–35‰). Data also indicate an increase in the prevalence and intensity of ***P. marinus*** associated with seasonal increases of water temperature. Preliminary studies do not indicate any relationship between the physiological condition of the host and the infection intensity of *Perkinsus marinus.* Data also indicate that, during periods of spawning when the oysters are in an apparently stressed condition, the prevalence and intensity of the infection is higher than during periods of gonadal inactivity and early development, although this may also be an artifact of temperature.

DEVELOPMENT OF A MUNICIPAL SHELLFISH HATCHERY AND NURSERY CULTURE FACILITY AS INTEGRAL COMPONENTS OF A PUBLIC RESOURCE MANAGEMENT PROGRAM. Stuart C. Buckner, Town of Islip, Department of Environmental Control, Islip, New York.

As part of the Town of Islip's comprehensive Shellfish Management Program which is aimed at replenishing depleted hard clam stocks in Great South Bay, an upflow nursery culture system was established in 1987 for the initial grow-out of *Mercenaria mercenaria* seed. The following year, a shellfish hatchery was developed and the nursery culture system was expanded to operate at a scale that would provide a significant resource benefit. Data on the population dynamics of the hard clam in Great South Bay, which is generated in the stock assessment phase of the Shellfish Management Program, were applied to the original design of the culture facility and will be instrumental in its continued development.

In the summer of 1987, eleven million clams were grown in the nursery system from a post-set size of less than 1 mm to an average size greater than 6 mm. Production of seed in 1988 is projected to be approximately 20 million, and at full-scale operation should be about 40 million clams of the 6–10 mm size range annually. Seed are transferred to field nursery systems for further grow-out to a size of 25–35 mm before being planted unprotected on the bay bottom in depleted areas of the shellfishery. The culture facility is described, growth and survival results from the nursery are summarized, and quantitative information on the natural population which was used to develop the mariculture project is presented.

REMOTE SETTING AND POST-SET STRATEGIES FOR GROWING *CRASSOSTREA VIRGINICA* IN VIRGINIA. Michael Castagna, College of William and Mary, Virginia Institute of Marine Science, Wachapreague, Virginia; **M. C. Gibbons** and **K. Kurkowski,** College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia.

Oyster production in Virginia has shown a drastic decline over the past three decades. In addition to a decline in marketable oysters, there is a shortage of wild (natural) seed oysters or spat. This shortage persists despite a variety of management strategies.

A pilot-scale experiment is being carried out to test the feasibility of supplementing wild seed harvest using hatchery-reared oyster larvae. The larvae are furnished to collaborating industry members for remote setting at the planting site in tanks of filtered seawater containing shell cultch. The spat is then held for a hardening period in some type of intertidal or off-bottom nursery system. After the spat reach a sanctuary size (about 3 cm), they can be planted in a growing area similar to natural wild seed.

A second part of the experiment is to test nursery methods for growing the post-set larvae to sanctuary size. Spat set on cultch or

cultchless are being grown in different nursery systems, including upwellers and tray and trestle systems. Trays are being held intertidally or lifted for weekly drying periods to control fouling and reduce predation.

Preliminary experiments indicate that intertidal exposure (air drying) increases survival.

EVALUATION OF THE EFFICACY OF A COMMERCIAL MICROENCAPSULATED DIET FOR GROWTH OF JUVENILE AMERICAN OYSTERS. Fu-Lin E. Chu, and **Mary C., Gibbons,** Virginia Institute of Marine Science, School of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Development of a successful artificial diet for oyster larvae and spat, to ultimately replace the expensive algal food, has been the goal of the shellfish industry. This paper will report the results of two feeding experiments in which juvenile oysters (shell height: 6.95 ± 1.0 mm, dry wt.: 58.83 ± 19.82 mg) are grown on a commercial microencapsulated diet (Frippak® microencapsulated feed (2.5–20 μm), England). Food value of the Frippak® diet is assessed by spat growth (increases of dry weight, ash weight (inorganic material) and organic weight). The controls consist of spat fed algal diets (*Tetraselmis suecica, Dunaliella tertiolecta* and Tahitian strain of *Isochrysis galbana* (T-ISO)) and unfed spat. Spat were reared on nylon mesh in air-lift upwelling columns (silo) in 20 l buckets with filtered (10 and 1 μm) estuarine water. One experiment has been carried out. Spat fed 100% Frippak diet were found to increase dry weight (DW, 17%), ash weight (AW, 14%) and organic weight (OW, 166%). These increases were approximately 20%, 18% and 62% of DW, AW and OW, respectively, of controls fed on a full algal diet (algal control, 200 cells/μl (50% of *D. tertiolecta* and 50% of T-ISO)). When the microencapsulated diet was substituted with 25% or 50% of the amount (number of cells) of algae fed to the algal controls, higher spat DW (47–52% higher), AW (44–51% higher) and OW (10–24% higher) were obtained. Unfed spat did not show any growth at all.

DESCRIPTION OF A NEW SAMPLING GEAR FOR JUVENILE SNOW CRAB, *CHIONOECETES OPILIO*. Francis Coulombe, Direction de la recherche scientifique et technique, Ministère de l'agriculture, des pêcheries et de l'alimentation du Québec, C.P. 1070, Gaspé, Canada; **Arthur Mauger,** Direction de la recherche scientifique et technique, Ministère de l'agriculture, des pêcheries et de l'alimentation du Québec, C.P. 340, Grande-Rivière, Canada.

In order to get sound management of Gulf of St. Lawrence's economically important fisheries for the snow crab, *Chionoecetes opilio*, a new type of demersal sampler was designed. Young snow crabs are distributed on a wide variety of grounds and usual sampling gears have been proved to be not totally efficient on each ones. The ultimate goal of this research was to obtain precise abundance estimates and size frequency distributions usable in forecasting recruitment to the fishery.

The prototype which is merging characteristics from a "Digby" scallop drag and a beam trawl is described in detail concurrently with an analysis of the criteria which lead to the actual concept. A preliminary assessment of its performance and efficiency was undertaken in 1985. The results were quite promising since individuals with size varying from 4–132 mm in carapace width have been caught on different types of substrates and density estimates agreed with data obtained by other sampling gears. Future research needs are briefly discussed.

DOES TIDAL ZONATION AFFECT THE INTENSITY AND INCIDENCE OF *PERKINSUS MARINUS* IN JUVENILE AMERICAN OYSTERS IN VIRGINIA? Mary C. Gibbons and **Fu-Lin E. Chu,** Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia.

The intertidal zone is better than the subtidal zone for the nursery of American osyters, *Crassostrea virginica*. Oysters exhibit higher survival and faster growth in the intertidal zone due to less predation and fouling. In 1986–1988, there were high mortalities of oysters in Virginia due to the protozoan *Perkinsus marinus*. The mortality of juvenile oysters in subtidal and intertidal zones was determined to be related to the incidence of *P. marinus* infection. The relationship of infection with tidal zonation in Virginia is not evident. This study investigated the incidence and intensity of *P. marinus* infections in juvenile oysters (one year old) held in intertidal and subtidal zones.

Spat, a subpopulation of which was determined to be free of *P. marinus*, were placed in cages in both the subtidal and intertidal zones at Wachapreague and Gloucester Point. Samples of 20 oysters were collected monthly from all cages at both sites. Growth of oysters was determined through measurement of shell height. Survival was determined by number of live spat. Oysters were examined for incidence and intensity of *P. marinus* using the Ray technique.

Preliminary results, from spat samples collected over three months, revealed that *P. marinus* was not present in spat collected from Wachapreague. Spat from Gloucester Point were found to have *P. marinus* infection. Zonation did not appear to influence the incidence and intensity of *P. marinus* in spat placed at Gloucester Point.

COMPARISON OF ENUMERATION TECHNIQUES FOR EYED LARVAE OF THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*. Mary C. Gibbons, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point,

Virginia; **Billie Jean Kemp,** Department of Biological Sciences, Mary Washington College, Fredericksburg, Virginia.

Eyed larvae of the American oyster, *Crassostrea virginica*, are shipped to remote setting sites by placing larvae in damp Nitex and paper towels held within a cooler with refrigerant gel packs. The numbers of eyed larvae need to be determined prior to shipment. The traditional method of determining numbers of bivalve larvae involves using a microscope to count the number of larvae in a subsample taken from a larger sample of known volume. This study compared three methods for enumeration of eyed larvae of *C. virginica* based on the settled volume, larval wet weight, and microscopic counting of subsamples.

Eyed larvae were sieved from cultures and retained on a 202 μm screen. The number of larvae was determined by counting using the technique of Loosanoff and Davis. The volume of eyed larvae was determined by allowing larvae to settle within an Imhoff cone. The wet weight of larvae was measured on an electronic balance.

Wet weight (g) and volume (ml) of eyed larvae were both found to be significantly correlated ($p < 0.0001$) to number of eyed larvae. Weighing and volumetric methods are simple and easy to perform; however, direct counting of larvae also provides the advantage of checking the quality of eyed larvae.

THE NATIONAL SHELLFISHERIES ASSOCIATION: EIGHTY YEARS OF FOSTERING SHELLFISH SCIENCE. Jeffrey Kassner, N.S.A. Membership Committee, % Town of Brookhaven, Division of Environmental Protection, 3233 Route 112, Medford, New York.

The National Shellfisheries Association (NSA) traces its origin to the formation of the National Association of Shellfish Commissioners (NASC) in 1909. The intent of the NASC was to promote molluscan shellfish science and to consider the "practical aspects" of the shellfish industry. The NASC grew rapidly and in 1930, to reflect the increased activity of shellfish scientists, was reorganized into the National Shellfisheries Association. Today, NSA has over 800 members in the United States, Canada, and eighteen other nations, representing government, academia, private industry, and individuals interested not only in molluscan, but also crustacean shellfish biology, ecology, and fisheries.

The original official publication of NSA was the *Proceedings of the National Shellfisheries Association*, which was published annually. In 1981, it was replaced by the *Journal of Shellfish Research*. All NSA members receive the *Journal* which is published twice a year, with occasional special issues. In addition, NSA publishes a quarterly newsletter to keep its members informed on Association affairs.

A long-standing constitutional tradition of NSA is its annual meeting. At the meeting, researchers can present papers describing their most recent findings and discuss matters of mutual interest. On average, meeting attendance is over 200, with nearly 90 papers presented on such topics as genetics, diseases, ecology, aquaculture and fisheries management. The annual meeting is held in different coastal cities and has recently been held in Seattle, Washington; Halifax, Nova Scotia; and New Orleans, Louisiana. Future meetings are planned for Williamsburg, Virginia and Portland, Maine.

Membership in the National Shellfisheries Association is open to all. NSA dues are $30.00/yr. ($20.00 for students). To join or for more information, please contact the NSA Secretary–Treasurer Dr.Thomas Soniat, % Department of Biological Sciences, University of New Orleans–Lakefront, New Orleans, Louisiana 70148.

DESIGN AND PERFORMANCE OF A SALTWATER LOW DISSOLVED OXYGEN TEST SYSTEM. D. C. Miller, D. E. Body, J. C. Sinnet US EPA; **S. Poucher** and **J. Sewall,** SAIC, Narragansett, RI

Dissolved oxygen (D.O.) concentration in marine systems are a major limiting factor, yet information on D.O. requirements of marine species is largely lacking. This is in part due to the lack of reliable apparatus. Our system was designed for flow-through acute and chronic tests to develop data for marine D.O. water quality criteria. Initial specifications included the capability to select six D.O. treatments regulated over the range of 0.5 mg/L to saturation to ±0.1 mg/L, a total flow rate of 4 gal./min., and operational stability for at least 30 days. The system is comprised of a vacuum degassing unit, reservoirs for saturated and low D.O. water, and an electronic proportioning system which mixes water from these reservoirs to provide five reduced D.O. treatments plus a saturated control. System performance demonstrates that D.O. is maintained at concentrations ranging from 0.1/L to saturation with a coefficient of variation 10% of the mean for the test duration.

Results of acute tests with winter flounder (*Pseudopleuronectes americanus*) include a mean LC50 of 1.9 mg D.O./L for late embryo to hatch stage, 1.5 mg/l for four-day larvae, and 1.4 mg/L for 2 cm (TL) juveniles; for juvenile sand shrimp (*Crangon septemspionsa*) a mean LC50 of 1.6 mg D.O./L; and for 2 cm surf clam (*Spisula solidissima*) a mean LC50 of 0.6 mg D.O./L. A 28-day chronic exposure of Atlantic silverside (*Menidia menidia*) resulted in 47% reduction in growth at 3.9 mg D.O./L.

TESTS FOR POSSIBLE RELATIONSHIPS BETWEEN GENETIC VARIABILITY AND LEVELS OF PARASITISM BY *PERKINSUS MARINUS* IN *CRASSOSTREA VIRGINICA*. Thomas M. Soniat, James M. Grady and **James S. Rogers,** Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana.

Ten populations of American oysters (30/population) were

sampled from Biloxi Bay, Mississippi westward to Galveston Bay, Texas. Adductor muscle tissue was used to determine level of infection of *Perkinsus marinus*, and to assess allelic variation using standard starch gel electrophoresis. Of the 23 loci examined, 12 showed allelic variation. The 7 most variable loci, Pgdh, Gpi, Pep-1, Lap-1, Pgm, Mpi, and Pep-2, were used to test the hypothesis that allelic variation was related to parasitism by *P. marinus* (a known cause of oyster mortality).Chi-square tests revealed no significant relationships between the frequency of individual alleles and level of parasitism. Mean heterozygosities of individuals were calculated, and a Kendall tau (τ) correlation was computed to test the relationship between heterozygosity and level of parasitism. Infection levels tended to be lower in oysters that exhibited higher levels of heterozygosity ($\tau = -0.087$), yet the relationship was not statistically significant at the $p \leq 0.05$ level ($p = 0.077$).

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COVER PHOTO: Hard clams (*Mercenaria* spp.) and intertidal oyster (*Crassostrea virginica*) reef in the northern Mosquito Lagoon on the east coast of Florida. Photo courtesy of Ray Grizzle.

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TOXIC ALGAL BLOOMS: HAZARDS TO SHELLFISH AND INDUSTRY

Proceedings of a special symposium held during the annual meeting of the National Shellfisheries Association, June, 1987 in Halifax, Nova Scotia.

Sponsored by:

National Coastal Resources Research and Developmental Institute
Hatfield Marine Science Center
2030 S. Marine Science Drive
Newport, Oregon 97365 USA

Convened and edited by:

Sandra E. Shumway

PREFACE

Toxic algal blooms are cosmopolitan phenomena and their impact on shellfish resources is profound. The problem is not a new one; red-tides have been recorded since biblical times. Not only do these outbreaks pose a threat to public health (numerous deaths have been attributed to paralytic shellfish poisoning over the years), they are responsible for large fish kills, destruction of other marine life and they result in great economic hardship to the coastal fishing industries.

The sources of these toxic blooms have been most commonly associated with members of the Dynophyceae, i.e., dinoflagellates. There have been many studies and symposia which have focused on the most predominant species of toxic dinoflagellates, e.g., LoCicero (1975), Taylor and Seliger (1979), Anderson et al. (1985) and Dale et al. (1987). The problems associated with toxic algal blooms are no longer limited to the dinoflagellates and are becoming increasingly severe on a global scale. Recent algal blooms attributed to a previously undescribed chrysophyte were responsible for the decimation of eel-grass beds and caused starvation and recruitment failure of commercially important bay scallop populations in Long Island waters (Cosper et al. 1987). These so-called 'brown tides' were also responsible for the near elimination of mussel populations in certain areas of Narragansett Bay (Olsen 1986, Seiburth et al. 1986). Areas of the Swedish west coast are currently being plagued by blooms of the prymnesiophyte, *Chrysochromulina polylepis,* previously unknown to the area. There is ever increasing evidence that outbreaks are increasing in intensity and distribution and the potential hazards to the shellfish industry are staggering. Shellfish monitoring programs designed to protect the general public have become a necessity in previously unaffected areas.

A special technical session devoted to toxic algal blooms and their impact on the shellfish industry was held as part of the annual meeting of the National Shellfisheries Association in Halifax, Nova Scotia in 1987. The principal objective of this symposium was to bring together scientists from various disciplines who were investigating different aspects of toxic algal blooms who might not otherwise have the opportunity to interact, e.g., chemists, economists and biologists, and to identify profitable areas of new research and collaboration. Contributions were also solicited from investigators who could not attend the conference to provide further insight and background information.

An interdisciplinary approach is important. Research and management are intimately linked in the formulation of regulations. Administrators cannot hope to develop and/or impose suitable and functional regulations without the input of knowledgeable researchers. Policies regarding public health and economic considerations must be based on sound scientific data if they are to be efficient, functional and accepted by the general populace.

This symposium would not have been possible without the financial support of the National Coastal Resources Research and Development Institute and to them we are extremely grateful. Through their efforts, the information gleaned from this conference will be disceminated to audiences not normally served by the scientific literature. It is hoped that the papers presented here will not only advance our scientific knowledge of the effects and impact of toxic algal blooms to the shellfish industry, but that they will stimulate new and fruitful collaborative studies of benefit to public health officials, the shellfishing industry and the scientific community.

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METHODS OF ANALYSIS FOR DSP AND PSP TOXINS IN SHELLFISH: A REVIEW

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ABSTRACT The accumulation of dinoflagellate derived toxins in molluscan shellfish represents a serious health threat if proper control measures are not implemented. In many areas of the world, the primary concern is Diarrhetic Shellfish Poisoning (DSP) and Paralytic Shellfish Poisoning (PSP). Regulatory agencies around the world have instituted testing programs for DSP and PSP that rely on the availability of rapid, reliable analytical procedures for the DSP and PSP toxin in shellfish tissue. Currently, mouse bioassays are the primary testing methods, but several newer techniques including immunoassays, binding assays and High Performance Liquid Chromatography (HPLC) methods are being developed. Included is a brief discussion of DSP and PSP with an emphasis on traditional and emerging analytical methods.

KEY WORDS: diarrhetic shellfish poisoning (DSP), paralytic shellfish poisoning (PSP) toxins, methods of analysis

INTRODUCTION

The periodic development of toxicity in normally non-toxic seafoods presents serious problems to harvesters, seafood processors, consumers and regulatory agencies. In a majority of cases, the toxicity stems from the presence of toxins derived from the marine food web. The three most common of these syndromes are Ciguatera, Diarrhetic Shellfish Poisoning (DSP) and Paralytic Shellfish Poisoning (PSP). Of these, the latter two impact primarily molluscan shellfisheries. It is now known that the primary producers of the toxins involved in both DSP and PSP are a number of species of dinoflagellates (unicellular photosynthetic algae), which as a group represent an important link in the marine food chain. Filter feeding shellfish are particularly prone to accumulation of dinoflagellate derived toxins since these algae serve as a primary food source.

Due to the sporadic nature of dinoflagellate blooms and the differing rates of uptake, release and metabolism of the toxins in various shellfish species, it is almost impossible to predict when and where shellfish will be toxic. For instance, in many areas of North America, mussels only become toxic from PSP in the summer months, when dinoflagellate bloom conditions occur, while several species of clams from the same locality can remain toxic year-round due to prolonged retention of the PSP toxins.

Insuring a non-toxic supply of shellfish to consumers is the responsibility of harvesters, processors and the regulatory agencies involved. The most effective means of accomplishing this is through controlled harvest of shellfish by either blanket closure of shellfish beds during certain times of the year or by instituting a shellfish toxicity monitoring program to pinpoint those areas and times when toxicity develops. In many parts of the world, monitoring programs have been developed to allow for year-round utilization of the shellfish resource. These monitoring programs rely heavily on the availability of rapid, accurate methods for determining the levels of the various toxins in shellfish tissue. For both PSP and DSP, the primary assay methods utilized currently are mouse bioassays involving intraperitoneal (ip) injection of an extract of shellfish tissue and observation of the mice for toxicity symptoms. Several alternative analytical methods are currently under development that may serve as a replacement for bioassay methods. Following is a brief discussion of both DSP and PSP with an emphasis on emerging techniques for analysis of the toxins involved.

Diarrhetic Shellfish Poisoning

Diarrhetic Shellfish Poisoning (DSP) is a recently described intoxication involving consumption of shellfish containing toxins produced by one of several species of dinoflagellates (*Dinophysis* spp., *Prorocentrum* spp). (Yasumoto 1985). A number of toxins have been isolated (Figure 1) with the okadaic acid derivatives (I–III, Figure 1) likely responsible for the primary diarrhetic symptoms. Very little is known currently about the uptake, distribution, metabolism and excretion of the DSP toxins in shellfish. Being fat soluble toxins, there does appear to be substantial bio-concentration of the toxins with a somewhat slow release rate. Currently, the majority of DSP problems have been reported in Japan and Europe but it is likely that, as our knowledge of DSP broadens, so will the reported incidences.

As with most marine toxins, the first analytical method developed for DSP was a mouse bioassay (Yasumoto et al. 1978) and this is the assay currently utilized for shellfish toxicity monitoring in most areas impacted by DSP. The mouse bioassay involves making an organic solvent extract of suspect shellfish tissue, and following evaporation, the residue is dissolved in a small volume of 1% Tween 60. The extract is injected ip into 20 g mice and the mice are observed for 24–48 hours for toxicity symptoms. One mouse unit (MU) is defined as the minimum amount of

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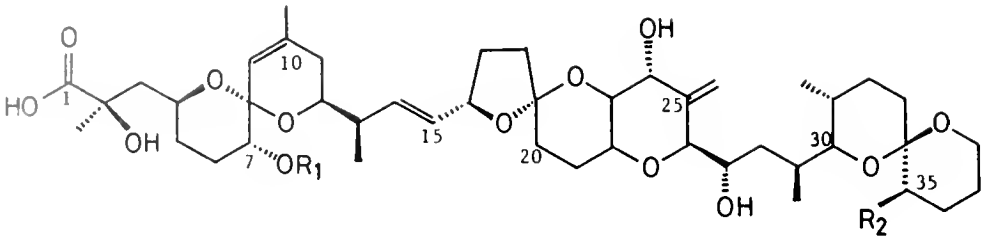
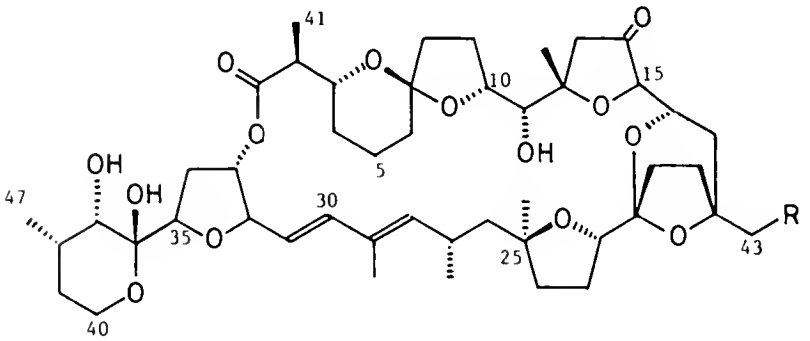


I okadaic acid : R_1 = H, R_2 = H
II dinophysistoxin-1 : R_1 = H, R_2 = CH_3
III dinophysistoxin-3 : R_1 = acyl, R_2 = CH_3



IV pectenotoxin-1 : R = OH
V pectenotoxin-2 : R = H

Figure 1. Structures of the DSP toxins. Reprinted from Yasumoto et al. 1984 with permission (copyright by ACS 1984).

toxin that kills a 20 g mouse within 48 hours. As with most bioassays, there are a number of drawbacks such as its somewhat poor sensitivity (the maximum allowable level in Japan is 0.5 MU/g shellfish tissue), it is time consuming and there can be interferences from extraneous material. Nevertheless, until an alternate testing procedure is developed that is proven to be more sensitive and reliable, it is likely that the mouse bioassay will continue to be widely used for DSP testing.

A number of alternative DSP assay techniques have been reported recently. Hamano et al. (1985) report a suckling mouse assay that is a direct measure of the diarrhetic effects of the toxins. The method involves intragastric administration of the shellfish extract followed by a measure of fluid accumulation in the intestine. In comparison to the regular mouse bioassay, this assay is reported to offer advantages in terms of speed, sensitivity and freedom from interferences. However, it is difficult to obtain a quantitative estimate of the amount of DSP toxin present and may be useful strictly as a qualitative test. Marcaillou-LeBaut et al. (1985) compared the regular DSP mouse bioassay and the suckling mouse assay and found that both tests showed somewhat poor reproducibility. Nevertheless, both testing procedures were reported to be useful in certain situations considering the lack of an alternate analytical technique.

Underdal et al. (1985) report a testing procedure for DSP based on cytotoxicity. The method involves measurement of lactate dehydrogenase leakage from rat hepatocytes following treatment with an extract of shellfish tissue. Their preliminary results indicate that the procedure may be applicable to shellfish toxicity monitoring, but further work would be required to characterize the response of the assay system.

The majority of work on DSP has been done in Japan by Yasumoto and co-workers. During these studies, a gas chromatographic method was developed for the okadaic acid based toxins (Murata et al. 1982). Although the method required either one or two derivatization steps to increase analyte volatility, it may be possible to refine the technique for use in shellfish toxicity monitoring. More recently, a method utilizing High Performance Liquid Chromatography (HPLC) has been reported (Lee et al. 1987). This method involves extraction of shellfish tissue with 80% methanol, purification of the extract by solvent partition and column clean-up followed by derivatization of the okadaic acid toxins with 9-anthryldiazomethane. The deriv-

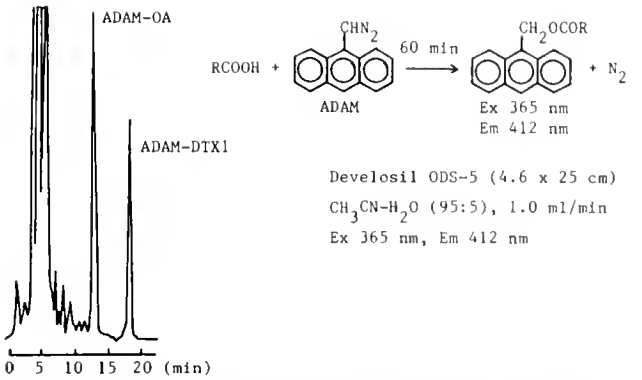


Figure 2. HPLC separation of okadaic acid (OA) and dinophysistoxin-1 (DTX1) by HPLC. Reprinted from Yasumoto (1985) with permission (copyright by Elsevier Sci. Pub. 1985).

atized toxins are then analyzed by HPLC utilizing a fluorescence detector (Figure 2). The method has advantages over the mouse bioassay in being more sensitive, specific and precise. Provided that good interlaboratory reproducibility can be demonstrated for this method, it is likely that the HPLC technique will provide a useful analytical procedure for routine shellfish toxicity monitoring.

Paralytic Shellfish Paisoning

Of the economically important seafood toxin problems, more is known about PSP than any of the others. PSP involves the accumulation of a number of alkaloid toxins (Figure 3) in shellfish. The primary producers of the PSP toxins are several species of dinoflagellates; *Protogonyaulax* spp., *Gymnodinium catenatum* and *Pyrodinium bahamense* (Taylor 1985). Additionally, the PSP toxins have been reported in crab in which the primary producer organism is as yet unknown (Noguchi et al. 1985) and it is well established that the toxins can be produced by a freshwater bluegreen alga; *Aphanizomenon flos-aquae* (Shimizu et al. 1985). It has become apparent that the presence of the PSP toxins is widespread with reports from temperate and tropical waters around the world. Filter feeding molluscan shellfish in many localities have been reported to contain the PSP toxins and management of this toxicity problem has assumed a global role as worldwide shellfish commerce increases.

A considerable base of knowledge has been established on the chemical and biochemical nature of PSP and is the subject of several recent reviews (Hall and Reichardt 1984, Shimizu 1987). It is apparent that the 12 sulfocarbamoyl and carbamate toxins (Figure 3) comprise the major "suite" of toxins produced by dinoflagellates. In addition, the decarbamoyl toxin derivatives can be present in shellfish due to enzymatic action on the corresponding sulfocarbamoyl or carbamate toxins (Sullivan et al. 1983). Consequently, any of the 18 toxins may be present in shellfish, depending on which toxins are produced by the particular strain of dinoflagellate in the local area, the presence of selective uptake and storage of the various toxins in the shellfish and any subsequent metabolism of the toxins in the shellfish tissue. This presents a very challenging situation to develop an analytical procedure for the PSP toxins, as any one or all 18 may be present in a shellfish sample and the method employed must be able to detect each toxin.

A detailed historical perspective on analytical techniques for the PSP toxins is the subject of a recent review (Sullivan et al. 1987) and will not be repeated here. Rather, a discussion is presented on those analytical methods that are either currently utilized or show promise as tools for shellfish toxicity monitoring programs. It is convenient to distinguish analytical methods as either an "assay" or an "analysis" technique in situations such as PSP where a number of biologically active compounds are involved (Hall and Reichardt 1984). An "assay" is a method in which a single result is obtained which is the sum total of the responses of all of the components present. A good example of this is the mouse bioassay in which a single response (usually time to death) is the cumulative result of a number of different toxins present in the sample. An "analysis" is a method in which the concentration of each toxin is determined individually. If a total toxicity value is desired, a calculation can then be made based on the individual toxicities of each component present. Depending on the requirements in a particular situation, either an "assay" or an "analysis" may be most applicable.

PSP Assays

By far, the most widely utilized technique currently in use for PSP is the mouse bioassay (AOAC 1984). This procedure is based on the pioneering work of Somer and Meyer (1937) which was later formalized (Medcof et al. 1947) and subjected to a collaborative study (McFarren 1959). The technique involves making an acid extract of shellfish tissue and injecting 1.0 ml of the extract into a standardized 20 g mouse. The death time (which is adjusted to the range, 5–15 minutes) is proportional to the amount of toxin in the extract and, by establishing a dose-response curve, is a fairly accurate measure of the total toxicity of the shellfish. The mouse bioassay has formed the basis for all the shellfish toxicity monitoring programs worldwide and has provided a high degree of public health protection.

Even though the mouse bioassay has proven to be quite useful, there are a number of serious drawbacks that have produced a nearly continual search for alternate analytical techniques. Among the disadvantages are a negative interference from high salt concentrations (Schantz et al. 1958), an inherent variability of $\pm 20\%$, the necessity of maintaining a large supply of mice and the growing concern on the appropriateness of using mammals for this type of work. Additionally, in a recent study (Park et al. 1986)

R1	R2	R3	Carbamate Toxins	N-Sulfocarbamoyl Toxins	Decarbamoyl Toxins
H	H	H	STX	B1	dc-STX
OH	H	H	NEO	B2	dc-NEO
OH	H	OSO_3^-	GTX I	C3	dc-GTX I
H	H	OSO_3^-	GTX II	C1	dc-GTX II
H	OSO_3^-	H	GTX III	C2	dc-GTX III
OH	OSO_3^-	H	GTX IV	C4	dc-GTX IV

R4: H_2N O− O

R4: H N O_3S^- O−

R4: HO−

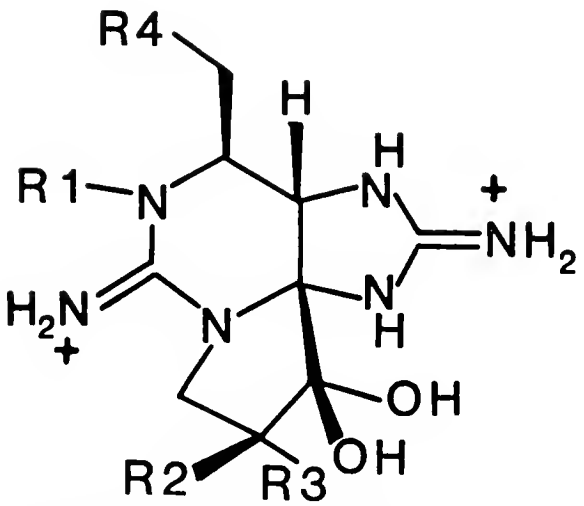


Figure 3. Toxins associated with PSP. Several (dc-NEO, dc-GTX I/IV) have not been reported in the literature, but are postulated to occur based on presence of the others.

excessive variability was reported for shellfish samples that contained high levels of toxicity.

A number of chemical assay techniques have been reported, but the oxidation/fluorescence method originated by Bates and Rapoport (1975) is by far the most promising (Figure 4). It is based on a measurement of the fluorescence of the oxidation products of the PSP toxins following alkaline oxidation with hydrogen peroxide. A number of investigations have been conducted to optimize the method and utilize it in shellfish toxicity monitoring programs (Childress 1980, Shoptaugh et al. 1981). Recently, Jonas-Davies et al. (1984) reported incorporation of the technique into an automated laboratory procedure. Overall, the oxidation/fluorescence technique is highly sensitive for the PSP toxins. However, its major drawback is that the various toxins do not fluoresce equally and for several of the highly toxic carbamate toxins (NEO, GTX I, GTX IV), the fluorescence is very weak. Nevertheless, in its present state of development, the method can provide a semi-quantitative measure of the PSP toxin content in shellfish and may provide a very rapid pre-screening method in a shellfish toxicity monitoring program.

A number of immunological based assay techniques for the PSP toxins have been reported (Johnson and Mulberry 1966, Carlson et al. 1984, Chu and Fan 1985). These techniques involve the application of standardized immuno-

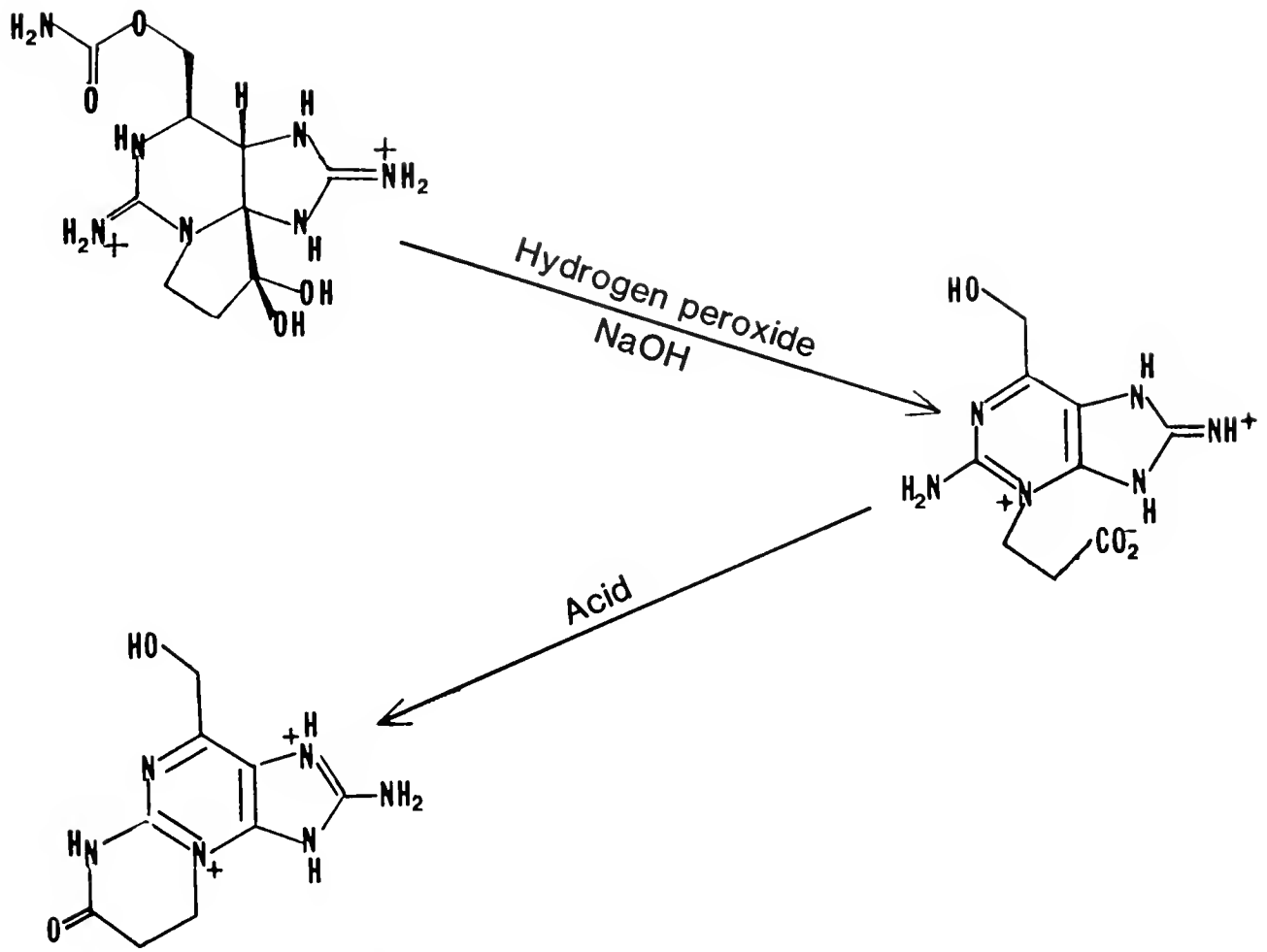


Figure 4. Alkaline oxidation of saxitoxin as reported by Bates and Rapoport (1975).

assay procedures to the PSP toxins. The difficulty in developing an immunoassay technique has been in obtaining a sufficient quantity of antibody, due partly to the high toxicity of the toxins involved, and the low molecular weight of the toxins. It has also been difficult to obtain an antibody that cross-reacts with all of the various toxins that may be present in the shellfish. Nevertheless, owing to the high specificity and sensitivity of immunoassay techniques, it is likely that further development may lead to a procedure useful as a semi-quantitative technique for the toxins.

Another assay technique that shows considerable promise is based on the pharmacological properties of the PSP toxins. The primary mode of action of the toxins in mammals is their binding to sodium channels in nerve cell membranes followed by interruption of normal depolarization. It has been found that the degree of binding is directly proportional to the degree of toxicity of the various PSP toxins. Therefore, by measuring the degree of sodium channel binding exhibited by the toxins in a shellfish extract, a very accurate estimate of the total toxicity of the shellfish could be obtained. Davio and Fontelo (1984) reported an assay based on this technique by measuring the amount of radiolabeled STX displaced from a rat brain membrane preparation. This assay was found to be extremely sensitive (ca 0.2 ppb STX) and selective for sodium channel blockers. Considering the high degree of correlation with total toxicity expected with this assay, it is likely that development work will continue with the aim of obtaining a rapid, accurate technique for measuring total shellfish toxicity.

PSP Analyses

In a situation such as PSP, involving multiple toxins, an "analysis" technique generally involves some sort of separation procedure. A wide variety of separation procedures have been reported including column chromatography (Shimizu et al. 1975, Hall 1982, Boyer et al. 1979), thin layer chromatography (Buckley et al. 1976, Hall 1982) and electrophoresis (Onoue et al. 1983, Boyer et al. 1979, Ikawa et

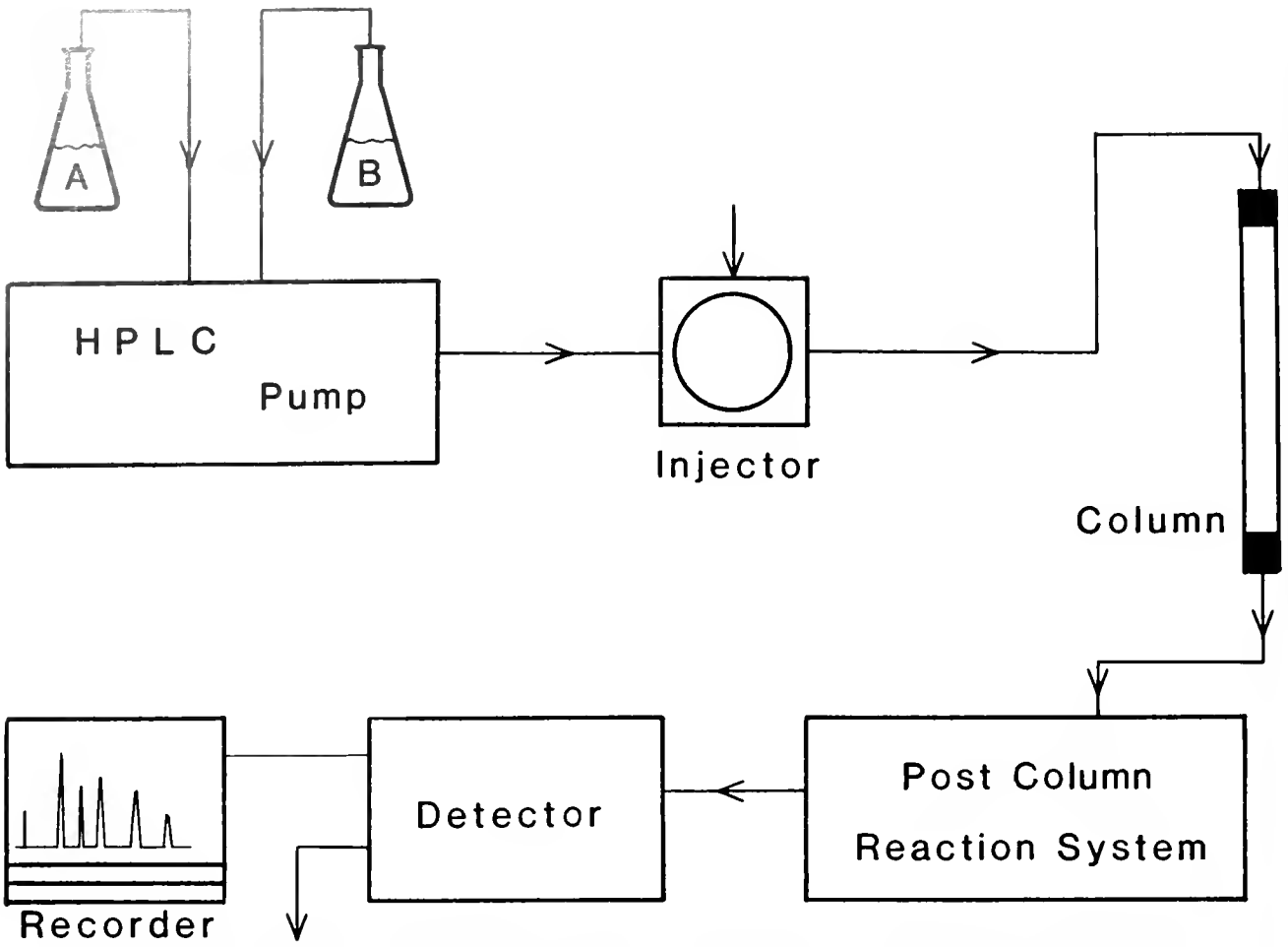


Figure 5. Flow diagram for the HPLC method for the PSP toxins utilizing post column oxidation and fluorescence detection.

al. 1985). While it is likely that several of these methods could be developed into procedures useful in shellfish toxicity monitoring programs, a method based on High Performance Liquid Chromatography (HPLC) has been reported that is directly applicable to shellfish monitoring (Sullivan and Iwaoka 1983, Sullivan and Wekell 1984, Sullivan et al. 1985a, b).

The HPLC method involves separation of the PSP toxins by ion-interaction chromatography with detection by fluorescence following post column oxidation (Figure 5). The method utilizes commercially available instrumentation and is based on established HPLC techniques. The detection technique employed in this method is based on the Bates and Rapoport (1975) fluorescence technique and the initial application of it into a continuous flow apparatus described by Buckley et al. (1978). However, it was found that, by substituting neutral periodate for the alkaline peroxide conditions in the post column reaction step, much greater sensitivity could be achieved for several of the PSP toxins (Sullivan et al. 1985a). Refinement of the column separation conditions has resulted in a system that is capable of resolving all 12 of the carbamate and sulfocarbamoyl PSP toxins (Figure 6). Sample preparation for the HPLC procedure is straightforward, involving simple acid extraction and filtration steps.

The HPLC method has been utilized in a variety of applications including research on the production of the PSP toxins in dinoflagellates (Cembella et al. 1987, Boyer et al. 1985a), the biochemistry of PSP in shellfish (Sullivan et al. 1983) and for elucidating the movement of the toxins up the food chain (Boyer et al. 1985b, Jonas-Davies and Liston 1985). In addition, several studies have addressed the correlation between the mouse bioassay and HPLC with the aim of utilizing it in shellfish toxicity monitoring programs (Sullivan et al. 1985a, Sullivan et al. 1985b). The correlation between the two techniques is good (Figure 7) and a cost comparison between the two techniques reveals that, for larger toxicity monitoring programs, costs per sample would be less using the HPLC (Sullivan et al. 1986). Considering current interest in the HPLC method, it is likely

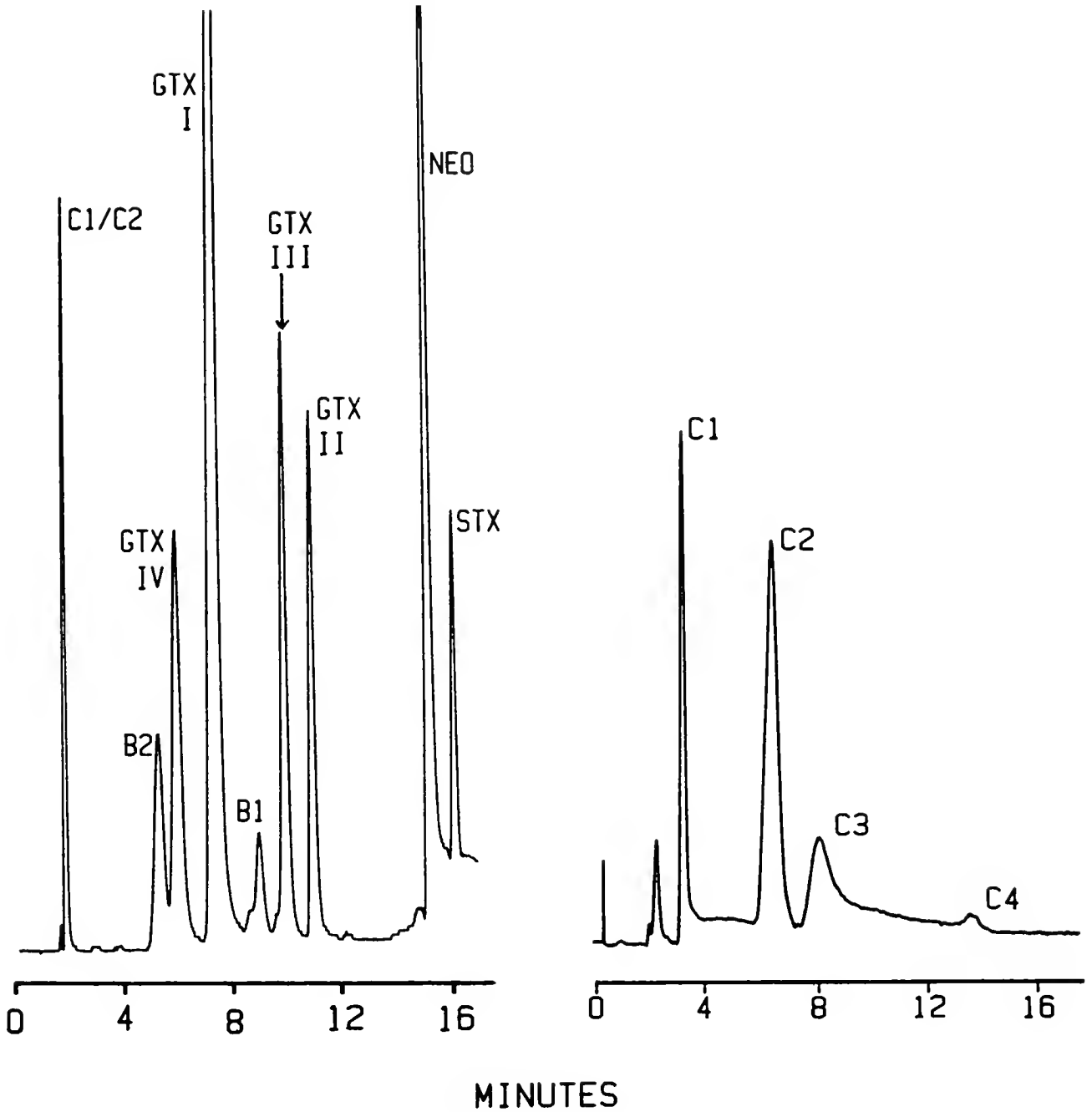


Figure 6. HPLC separation of the 12 carbamate and sulfocarbamoyl PSP toxins.

that it will be utilized in the future in shellfish toxicity monitoring programs.

CONCLUSIONS

Evidence in recent years indicates a worldwide distribution of DSP and PSP toxins in molluscan shellfish. Rapid and reliable analytical techniques are needed to conduct research and support shellfish toxicity monitoring programs in areas impacted by DSP and PSP. While mouse bioassays have proven to be effective tools for this work, several newer analytical techniques show promise as being faster, more sensitive and more accurate. Additionally, separation techniques such as HPLC can provide data on distribution of the various toxins which leads to a greater understanding of the biochemistry and chemistry involved. It can be expected that, as the utilization of these new analytical techniques increases, so will our understanding of these marine toxin problems.

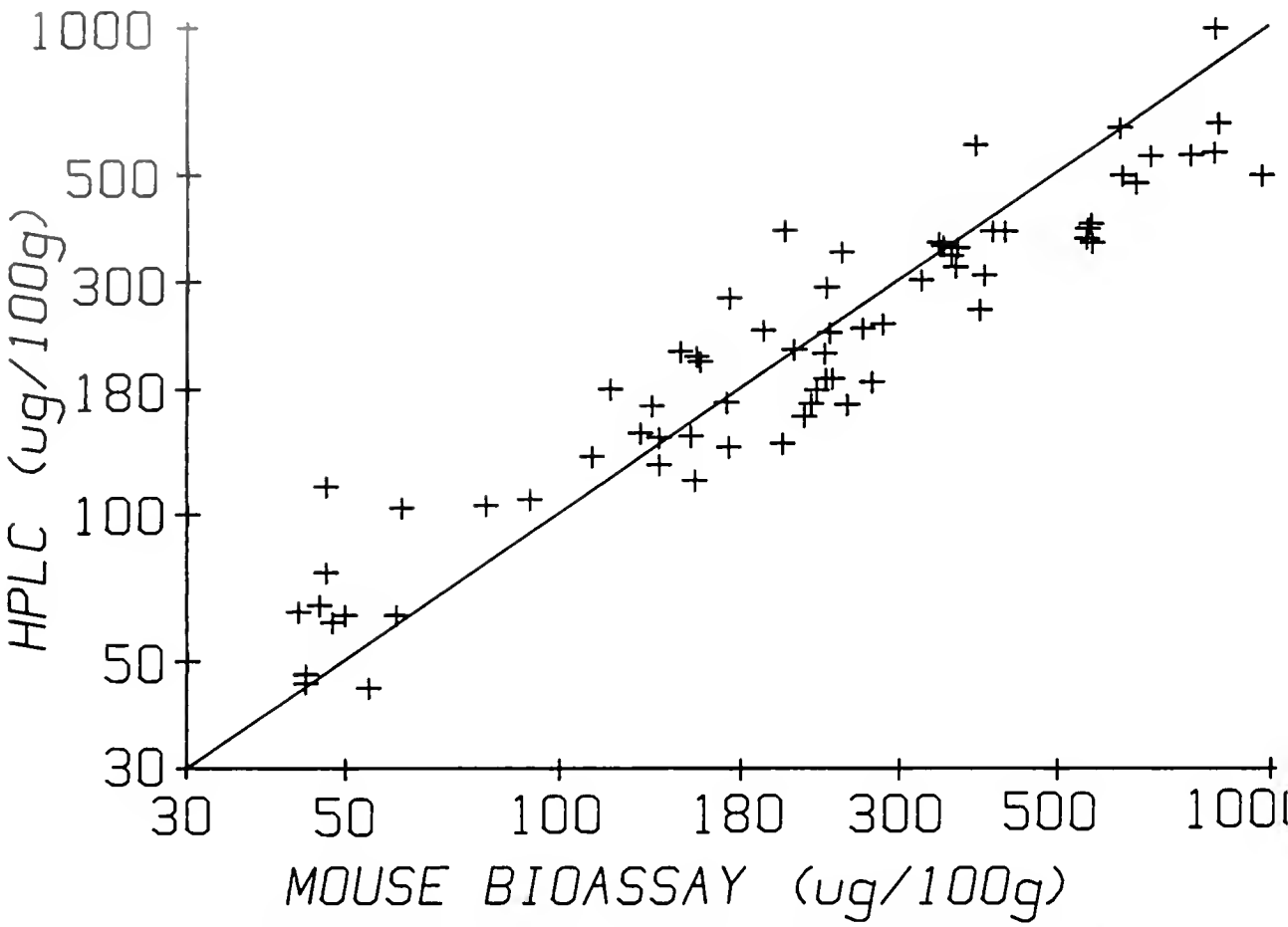


Figure 7. Correlation between the HPLC and mouse bioassay for the determination of PSP toxins in shellfish.

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SPATIAL DISTRIBUTION OF *PROTOGONYAULAX TAMARENSIS* RESTING CYSTS IN NEARSHORE SEDIMENTS ALONG THE NORTH COAST OF THE LOWER ST. LAWRENCE ESTUARY

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ABSTRACT The spatial distribution of resting cysts of *Protogonyaulax tamarensis* (Lebour) Taylor was investigated along the north shore of the Lower St. Lawrence estuary, within and adjacent to the frontal plume produced by the trans-estuarine freshwater outflow of the Manicouagan and Aux-Outardes rivers. Nearshore sediments sampled during the summer, prior to the development of significant concentrations of motile *Protogonyaulax* cells in the water column, yielded only low cyst concentrations. However, in autumn, several weeks after the disappearance of *Protogonyaulax* from the surface waters, cyst concentrations at the same stations were markedly elevated. Although the quantitative cyst distribution was rather variable, certain trends were noted. First, cysts were primarily associated with sediments dominated by fine-grained sand, but which also contained a substantial percentage of silt and clay. Second, the highest cyst concentrations were found at the downstream periphery of the front, and between the converging freshwater plumes of the Manicouagan and Aux-Outardes rivers. Finally, for the stations adjacent to this frontal plume, the highest cyst accumulations in autumn corresponded to areas characterized by the highest mean annual paralytic shellfish toxicity in shoreline molluscs. The results suggest that spatial distribution of dinoflagellate cysts and the consequent blooms in the St. Lawrence estuary are highly dynamic, and strongly controlled by water circulation patterns. The hypothesis that the toxic blooms which appear on the south shore may originate through exogenous transport of populations derived from cyst beds along the northern shore is further supported.

KEY WORDS: *Protogonyaulax, Gonyaulax*, dinoflagellates, red tide, paralytic shellfish poisoning, resting cyst, hypnozygote

INTRODUCTION

For many years, the toxic marine dinoflagellate *Protogonyaulax tamarensis* (Lebour) Taylor (also known as *Gonyaulax tamarensis, G. excavata, G. tamarensis* var. *excavata, Gessnerium tamarensis, Alexandrium tamarense* or *A. fundyense* by various authors) has been implicated as the source of paralytic shellfish poisoning (PSP) in eastern Canadian waters (Needler 1949, Prakash 1963, 1967, Prakash et al. 1971). It is now widely recognized that the cyclical development of dinoflagellate blooms forming toxic red-tides is often dependent upon the presence of *in situ* seed beds of hypnozygotic resting cysts (Steidinger 1975, Wall 1975, Anderson and Wall 1978, Anderson and Keafer 1985, Carreto et al. 1985). Accumulations of these dinoflagellate cysts have been observed in a variety of marine ecosystems, including offshore trenches and depressions, fjords, estuaries and shallow coastal embayments (Dale 1976, Dale et al. 1978, Anderson and Morel 1979, White and Lewis 1982, Balch et al. 1983).

In certain coastal and estuarine environments, transport of allocthonous populations of suspended cysts and motile cells to a localized site may also contribute to bloom formation (Anderson and Wall 1978, Seliger et al. 1979). Under favorable hydrodynamic conditions, the shoreward displacement of toxic *Protogonyaulax* populations can result in the contamination of onshore shellfish beds. This would normally be considered a natural phenomenon, subject to the dynamics of water mass transport, but concerns have also been expressed that human intervention, in the form of ship de-ballasting or the transfer of shellfish stocks, may also be a factor in the inadvertent introduction of "seed populations" of cysts or motile cells into previously uncontaminated areas (Anderson 1984).

Attempts to evaluate the potential risk of PSP contamination, particularly in highly dynamic marine ecosystems,

solely by following the distribution of motile cells in the water column are limited by the rapid response time required to track emphemeral bloom populations. Alternatively, use of historical shellfish toxicity data also sharply restricts predictive capacity, since shellfish toxin samples are usually obtained from only a relatively small number of key stations, which are assumed to be representative. Furthermore, since PSP toxins are subject to differential metabolism in molluscs, *a posteriori* toxicity determinations yield only net toxin levels remaining after an unknown period of intoxication and depuration. This provides neither detailed information regarding the density and toxicity of the *Protogonyaulax* bloom(s) responsible for the contamination, nor any means of evaluating their possible recurrence.

Frontal circulation mechanisms have previously been invoked to explain the occurrence of red-tide blooms of *Ptychodiscus brevis* (= *Gymnodinium breve*) along the west coast of Florida, and of *Protogonyaulax tamarensis* (= *Gonyaulax excavata*) in the coastal regions of Maine and Massachusetts (Seliger et al. 1979). Convergence zones have also been associated with high deposition of *Protogonyaulax* cysts in shallow embayments (Garcon et al. 1986), and, on a greater spatial scale, with the accumulation of cysts of *P. tamarensis* off the Argentine coast (Carreto et al. 1985), and those of *Gyrodinium uncatenatum* (Tyler et al. 1982) and *Gymnodinium pseudopalustre* (Tyler and Heinbokel 1985) in Chesapeake Bay.

Benthic cysts should represent more spatially stable populations than the transient blooms from which they may be derived. The fact that cysts can be collected and enumerated during non-bloom periods, offers, in principle, a potential means for the prediction of future PSP outbreaks. The resting cysts of *Protogonyaulax* are themselves toxic (Dale et al. 1978, Yentsch et al. 1980, Hurst and Yentsch 1981, White and Lewis 1982), and have been proposed as a direct cause of shellfish toxicity on the Atlantic coast (Yentsch and Mague 1979). Thus, information regarding the quantity and spatial distribution of toxic cysts in the sediments, when integrated with knowledge of hydrodynamic, chemical and biological factors in the water column, may provide a partial explanation for the timing, periodicity and persistence of toxic blooms, as well as the resultant contamination of shellfish resources.

Current and historical data on the distribution of shellfish toxicity along the north coast of the Lower St. Lawrence estuary (Therriault et al. 1985, Beaulieu and Ménard 1985, Cembella and Therriault 1988a, b) indicate that zones of high PSP toxicity are associated with the plume produced by the Manicouagan/Aux-Outardes river system. The present study was undertaken in an attempt to establish the relationship between the sediment characteristics in the region, shellfish toxicity in shoreline molluscs, and the spatial distribution of cysts within and adjacent to the core of the trans-estuarine front generated by this high freshwater outflow.

MATERIALS AND METHODS

Cyst Sampling and Preparation

The study area was situated along the north shore of the Lower St. Lawrence estuary, between Forestville and Godbout (Figure 1). Thirty stations (1–30) were sampled along the narrow shoreline plateau (<120 m depth); odd numbered stations were located at approximately 1–3 km from the coast, while even-numbered stations were situated at 3–6 km from shore. Three additional deep-water stations (41, 43 and 44) were sampled along a north to south transect across the Laurentian Channel off Forestville. In order to estimate cyst numbers present in the sediment, just prior to the initiation of the *Protogonyaulax* bloom, sediment sampling was carried out on the whole sampling grid between June 17 and July 1, 1986. Several weeks after the termination of the summer bloom (Cembella and Therriault 1988a, b), between October 10–13, 1986, the cyst sampling was repeated at the same stations. During cyst collection, data on standard oceanographic parameters were obtained by established routine analytical methods for: surface water temperature, salinity, *in vivo* chlorophyll *a* fluorescence, inorganic nutrients (NO_3 + NO_2, PO_4, and $Si(OH)_4$), Secchi depth, and wind speed and direction (as in Therriault and Levasseur 1985).

Cyst distributions in the sediments were established using a Shipek benthic grab (Wildco, Saginaw, MI) and a 67 mm (i.d.) gravity corer (Model 2171, Benthos, North Falmouth, MA). The sediment samples retained by the gravity corer were less reproducible, particularly in coarse substrate, than those from the Shipek sampler; they also showed more obvious compaction and disruption of the surface organic layer. Therefore, all cyst counts were based upon 250 cm^3 sub-cores from the Shipek samples, to represent approximately the top 5 cm of sediment. The sediment surface water layer held in the sampling bucket was passed through a 73 μm Nitex net and added to the solid material. Samples were kept refrigerated (0–4°C) in the dark until analysis.

Sediment samples were homogenized manually by thorough stirring, then a 15 cm^3 subsample was suspended in 200 ml of ice-cold, filtered (0.45 μm) seawater. The suspension was disaggregated by probe-sonication (Heat Systems Model W220, Heat Systems, Farmington, NJ) for 2 min at 40% of maximum intensity (75 W), to separate the cysts from organic and inorganic aggregates. The sonicated suspension was poured across a 150 μm Nitex net filter mounted in a PVC cylinder, then a gentle stream of ice-cold filtered seawater was used to rinse fine particles through the net. The sieving process was repeated with a 73 μm Nitex mesh, to ultimately retain the cyst-containing

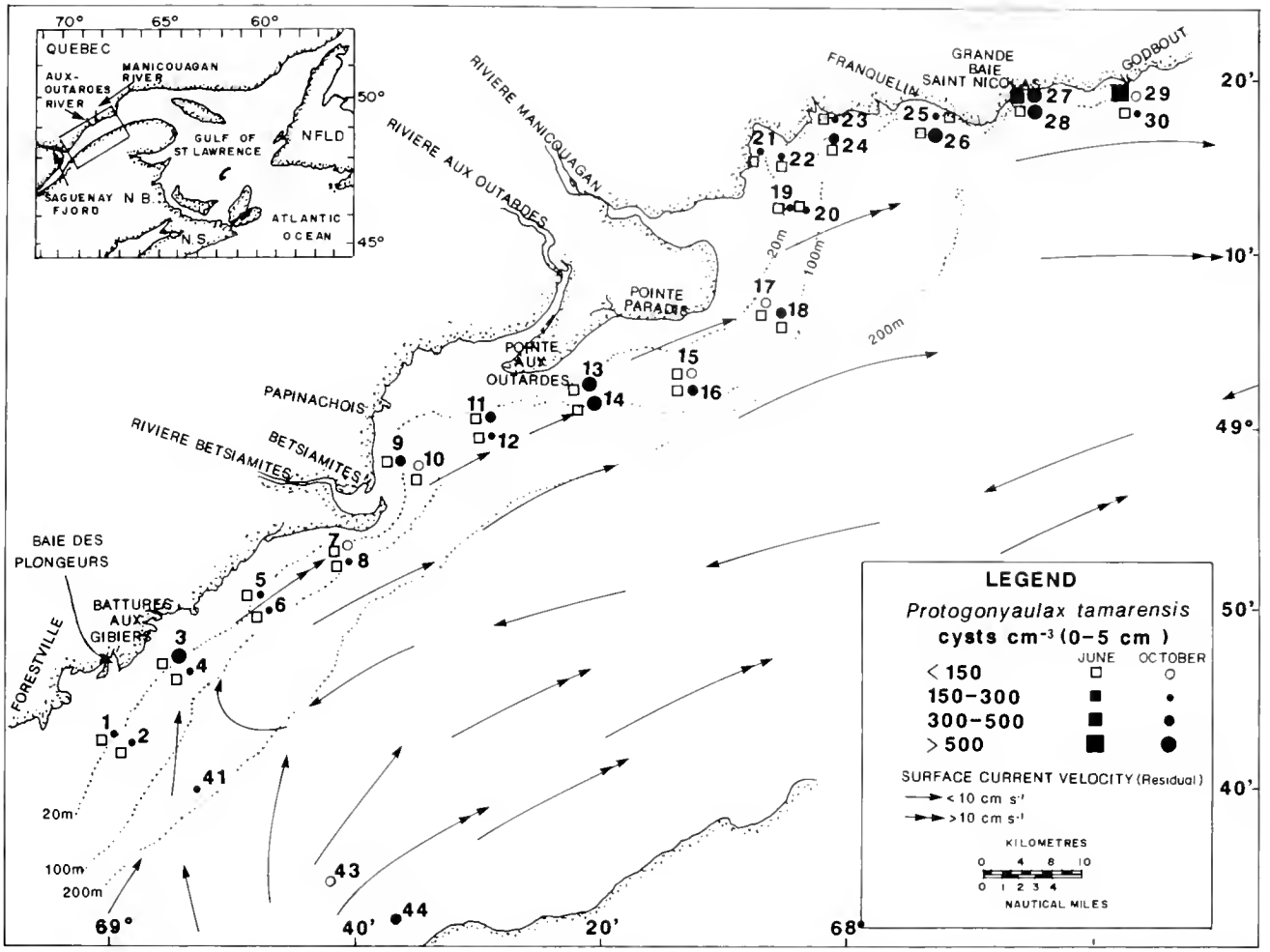


Figure 1. Location of sampling stations (1–30, 41, 43 and 44) and relative abundance of *Protogonyaulax* resting cysts during June and October 1986, in surface sediments of the Lower St. Lawrence estuary (Québec) (Generalized pattern of residual surface currents adapted from El-Sabh 1979).

fraction upon a 20 μm net. Microscopic analysis of the fine particles which passed through the 20 μm mesh showed that no *Protogonyaulax* cysts were lost by this sieving process. The 20 μm fraction was rinsed from the net and resuspended in 20 ml of filtered seawater. The sample was mixed thoroughly and divided in half. A "live" sample and a sample preserved by the addition of several drops of concentrated (37%) formalin were retained in the dark at 4°C for future microscopic observation.

The cysts of *Protogonyaulax tamarensis* were identified according to descriptions given in the literature (Dale 1977, 1979, Anderson and Wall 1978, Turpin et al. 1978, Benavides et al. 1983, Fukuyo 1979). Cysts were enumerated by counting aliquots of vortex-mixed samples in triplicate, in 0.1 ml Palmer-Maloney chambers under phase-contrast microscopy (200×). The precision of triplicate cyst counts from surface sediments at the same station was strongly affected by the cyst density: for stations with >500 cysts cm^{-3}, the coefficient of variation (C.V.) ranged between 4–10%, while for stations with <150 cysts cm^{-3}, the C.V. varied from 18–100%.

Photographs of certain specimens were made at 400× using phase-contrast microscopy (e.g., Figure 2). Epifluorescence microscopy was also used to observe the autofluorescence emitted following chloroplast excitation with UV light (Wild-Leitz filter system A2, excitation BP 270–380 nm, suppression BP 410–580 nm).

Granulometric and Elemental Analysis of Sediments

Sediment grain size was determined by a conventional fractionation method (Rivière 1977), which consisted of sieving the sediments through metal screens of 150 μm and 63 μm, to subsequently obtain the dry weight of each fraction retained. The rinse water was collected, and the fine-grained silt and clay was resuspended by agitation. After diluting the suspension to 500 ml, two sub-samples were taken at two hour intervals using an Andreasen pipette. The silt and clay fractions were separated, according to Stokes'

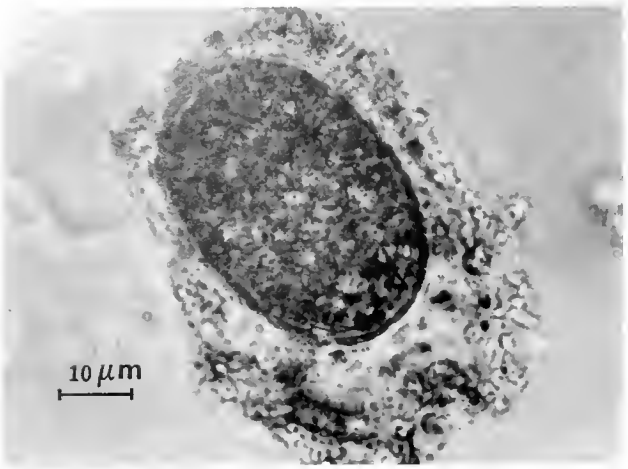


Figure 2. Light micrograph (Mag. 400×) of a recently formed resting cyst (hypnozygote) of *Protogonyaulax tamarensis* showing the typical surface mucilaginous sheath and uniform microgranular ultrastructure.

law applicable to the settling rate of particles, and their total dry weight was determined. The sediment grain size was expressed as: $\Phi = 10 \times -\log_2$ mean grain diameter (in mm), with fractions operationally defined as gravel (>1 mm), sand (62.5 μm–1 mm), silt (3.9–62.5 μm) and clay (<3.9 μm).

The elemental composition (C/H/N) was determined from approximately 5 g wet weight of sedimentary material from each station. The samples were dried (24 h at 40°C) and the dry weight was determined. The material was sieve-fractionated as described above, and then concentrated by centrifugation (15 min at 3000 × g). The fractions were re-dried (24 h at 40°C) and ground to a fine powder. To minimize the hygroscopic effect on small particles, fractionated samples were dried for a further 24 h (60°C). Sub-samples (15 mg) of this fractionated material were analyzed for total C and N content using a CHN analyzer (Perkin-Elmer Model 240B).

Mouse Bioassays on Contaminated Molluscs

Pooled samples (100 g wet weight) of shellfish meat from the soft-shelled clam, *Mya arenaria,* were obtained from intertidal sites adjacent to the cyst-sampling stations, at Baie des Plongeurs, Battures aux Gibiers, Betsiamites, Papinachois, Pointe-aux-Outardes, Pointe Paradis, Franquelin and Grande Baie St-Nicolas (Figure 1), and submitted for mouse bioassays (Microbial Hazards Division, Dept. of Health and Welfare, Ottawa). Mouse bioassays were performed according to the AOAC (1984) method, by injecting six female (20 g) mice per assay; reference saxitoxin (STX) (Division of Microbiology, Food and Drug Administration, Cincinnati, OH) used as the calibration standard. Toxin levels in μMouse Units, as determined by death time, were converted to saxitoxin equivalents (STXeq) using the conversion factor: 1 Mouse Unit = 0.215 STXeq.

RESULTS

The resting cysts of *P. tamarensis* from the St. Lawrence estuary (Figure 2) were comparable in linear dimensions (length: 49.6 ± 2.8 SD μm, width: 30.6 ± 1.2 SD μm, n = 30) and general morphology to specimens from other locations on the Atlantic coast of North America, including the Bay of Fundy (White and Lewis 1982), certain shallow marine ponds in Massachusetts (Anderson and Wall 1978, Anderson 1980), and the Gulf of Maine (Yentsch et al. 1980). The cysts were not readily distinguishable from those belonging to the "tamarensis" species complex (Taylor 1979) from the coast of Norway (Dale 1977) and from Japan (Fukuyo 1979, 1985). The St. Lawrence estuary cysts were, however, somewhat larger than those identified as *P. tamarensis* from the Pacific coast of North America (Turpin et al. 1978).

Details regarding the environmental conditions prevailing in the water column during the summer cyst sampling period from late June to early July have already been described in another publication (Cembella and Therriault 1988b). In summary, mean surface temperature within the core of the Manicouagan/Aux-Outardes river plume (Stations 9–22) rapidly increased from approximately 6°C at the end of June, to nearly 12°C after the first week of July. During the same period, mean surface salinity decreased dramatically from 30.6 to 21.6‰ in this region.

The shallow surface pynocline evident at 4–8 m during late June deepened to approximately 10–15 m by July 7. Surface inorganic N concentrations in the upper 10 m of the water column varied substantially (range: 0.3–12 μM, mean: 3 μM), but did not appear to be limiting for phytoplankton growth in late June and early July.

Results from the Shipek sampling revealed the absence of *Protogonyaulax* cysts during late June at Stations 1–10 between Forestville and Papinachois, while at Stations 11–22, between Pointe-aux-Outardes and Baie Comeau, <30 cysts cm^{-3} were recovered from the surface sediments. Within the region between Baie Comeau and Godbout (Stations 23–30), cyst counts were also generally low, with the exception of two stations (Figure 1). At Station 27 (Grande Baie St-Nicolas), the relatively high cyst numbers (~400 cysts cm^{-3}) found in June remained similarly high in October (>500 cysts cm^{-3}); at station 29 (Godbout), the sediments were infested with cysts in June, however none were found in October.

There was evidence of depleted starch reserves in most of the cysts collected in June, and an abundance of the dark brown-pigmented microgranular material located at the poles, which is typical of mature cysts (Anderson 1980, Yentsch et al. 1980, Anderson et al. 1983). In fact, in certain "live" samples maintained for several days at 4°C,

then exposed to room temperature during preparation for microscopy, excysting cells (planomeiocytes) were observed exiting through fractured archeopyles, thereby breaking the obligate dormancy period. In cyst samples from Station 29, at the downstream periphery of the plume (Figure 1), motile cells were occasionally found swimming in the seawater overlying the sediment.

From early September to mid-October, mean surface water temperature decreased from approximately 8 to 5°C, while mean surface salinity declined only marginally from 27 to 25‰ in the plume-dominated region. Mean wind stress was low and variable, while prevailing winds tended to be westerly (Figure 3). Although freshwater output rate from the major river systems (Figure 4) did not exhibit any evident trend, the extent of the frontal zone created by the Manicouagan/Aux-Outardes river outflow in mid-October could be identified by the steep gradient of higher water temperature and lower surface salinity within the plume (Figures 5A and B). However, a region characterized by slightly lower surface water temperature, higher salinity, and elevated surface $NO_3 + NO_2$ concentrations, was evident off Pointe-Aux-Outardes (Figures 5A, B and C).

In mid-October, cyst concentrations were strikingly higher than in June at all stations along the north coast. Significant numbers of *Protogonyaulax* cysts were found at every station sampled during October, although the concentrations varied markedly. Analysis of the spatial distribution of cysts after the bloom revealed three localized areas of high cyst deposition (Figure 1):

1. Between Franquelin and Grande Baie St-Nicolas, adjacent to the downstream extent of the estuarine frontal plume, where the highest cyst numbers (>1500 cysts cm^{-3} at Station 28) were recorded,
2. Adjacent to the Manicouagan peninsula, between the convergent outflow of the Manicouagan and Aux-Outardes rivers,

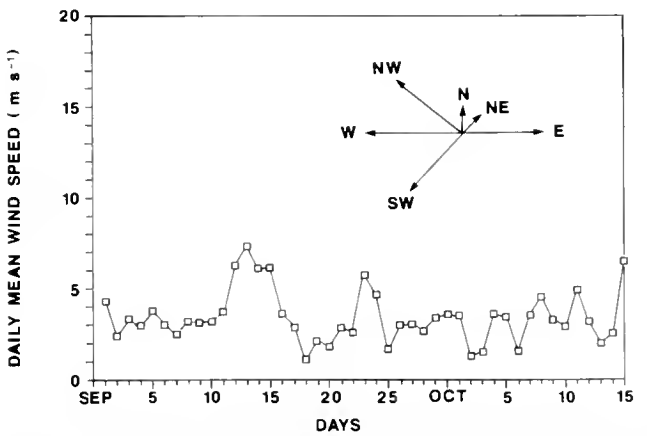


Figure 3. Mean wind speed and prevailing direction (% of time, computed daily) during and subsequent to the termination phase of the *Protogonyaulax* bloom.

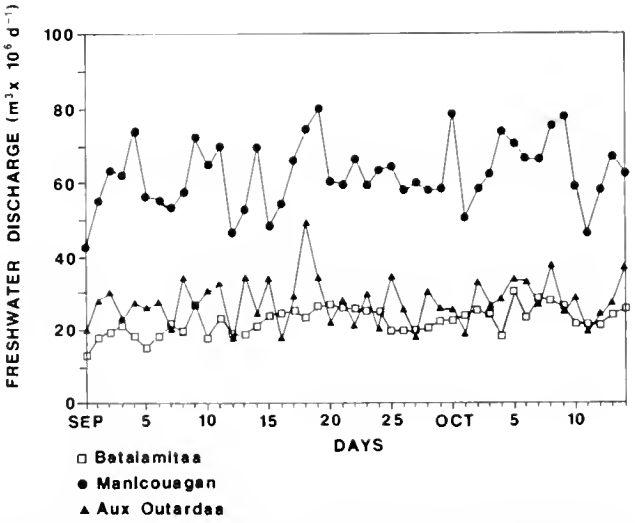


Figure 4. Daily freshwater discharge rate from three major rivers, Betsiamites, Manicouagan and Aux-Outardes, on the northern shore of the Lower St. Lawrence estuary (Québec).

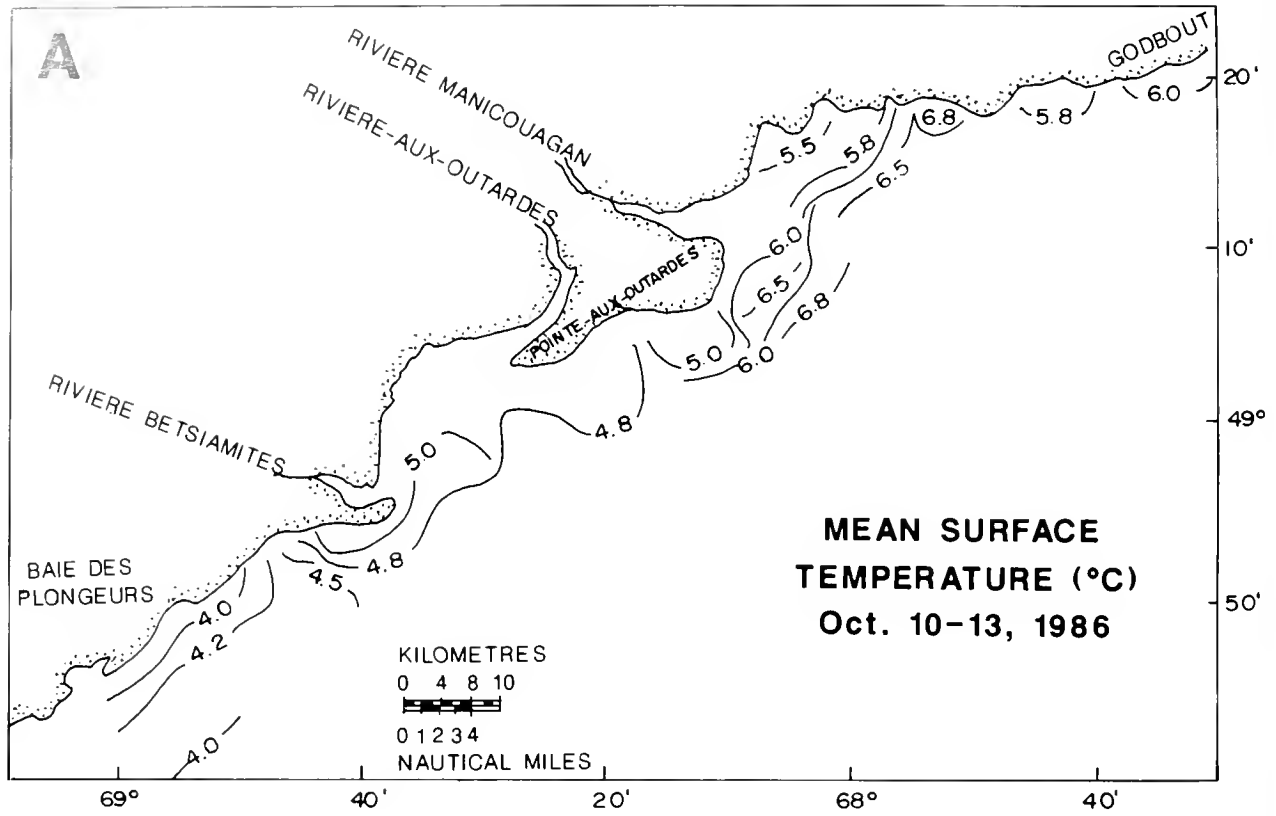
3. In shoreline sediments along the Battures aux Gibiers.

In both summer and autumn, the single trans-estuarine transect in the deeper water sediments of the Laurentian Channel between Forestville and Rimouski yielded only relatively low cyst levels.

The cysts collected in October were elongate, ellipsoid, smooth-walled and coated with a thick amorphous gelatinous layer (Figure 2). In contrast to the majority of the specimens collected in early summer, the external wall was rather thin, but clearly intact, and the cells were filled from pole to pole with translucent granular starch bodies. In most cysts, a centrally-located bright orange deposit of carotenoid pigments was visible. Fresh samples observed under epifluorescence microscopy also frequently exhibited a brilliant red autofluorescence when excited by UV light.

Granulometric analysis of the sediments obtained in October revealed that, typically, the surface material along the shoreline plateau consisted principally of fine-grained sand (range: 23.3–97.3%), with little gravel (Figure 6). The combined percentage of silt and clay (range: 1.8–75.6%) was usually less than that of the sandy fraction. Correlation analysis of sediment size fractions and cyst numbers for all sampling stations did not reveal any significant relationship ($p \leq 0.05$, n = 33); for % sand vs. cyst numbers, the Pearson product-moment correlation coefficient (r) was 0.08, while for % silt/clay vs. cyst numbers, r was −0.05. The representative grain-size frequency histograms of several stations (Figure 6) also showed that although sand was characteristically the dominant surface sedimentary material where cysts were found, grain size was not a good predictor of cyst abundance.

Attempts to correlate cyst concentrations with elevated



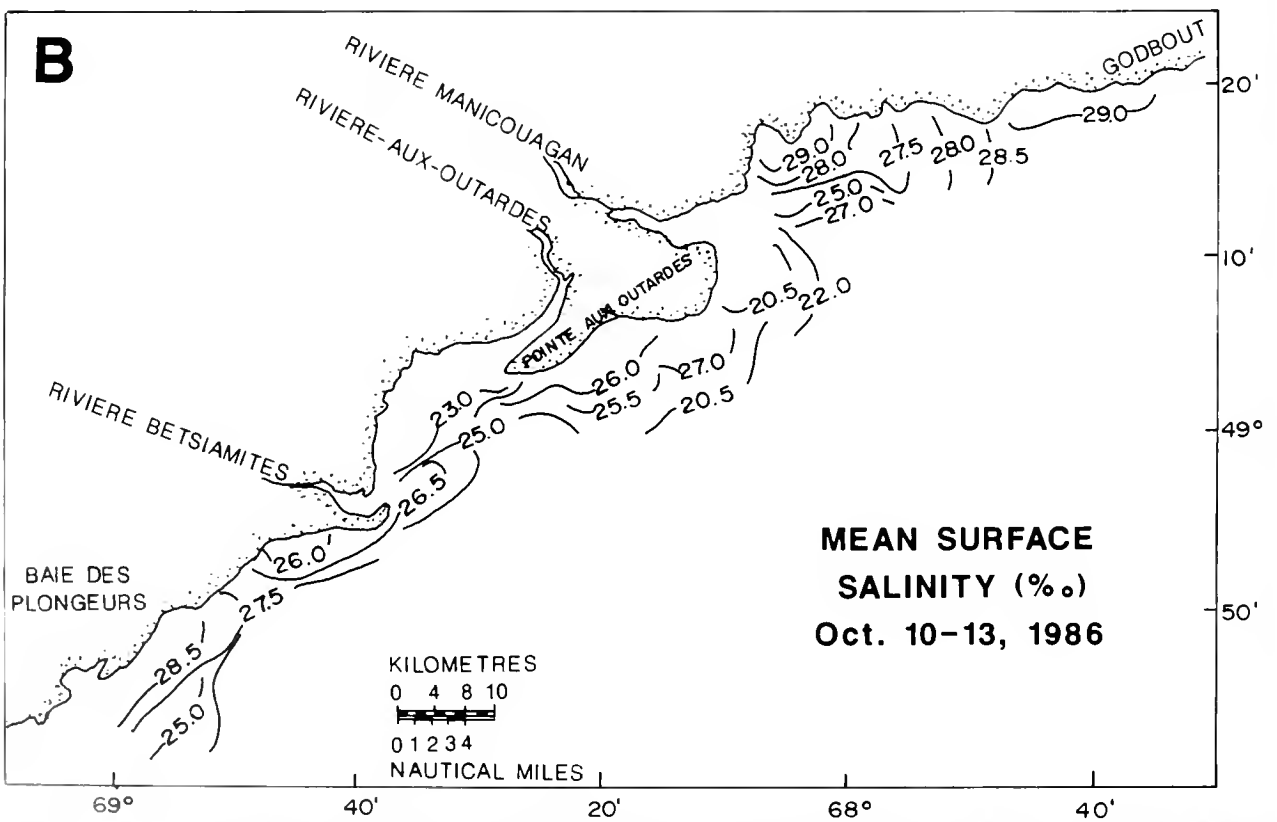


Figure 5. A) Mean surface temperature, B) salinity and C) dissolved inorganic nitrogen ($NO_3 + NO_2$) concentrations during the October 1986 sediment sampling period, within and adjacent to the river plume-influenced zones on the north coast of the Lower St. Lawrence estuary (Québec).

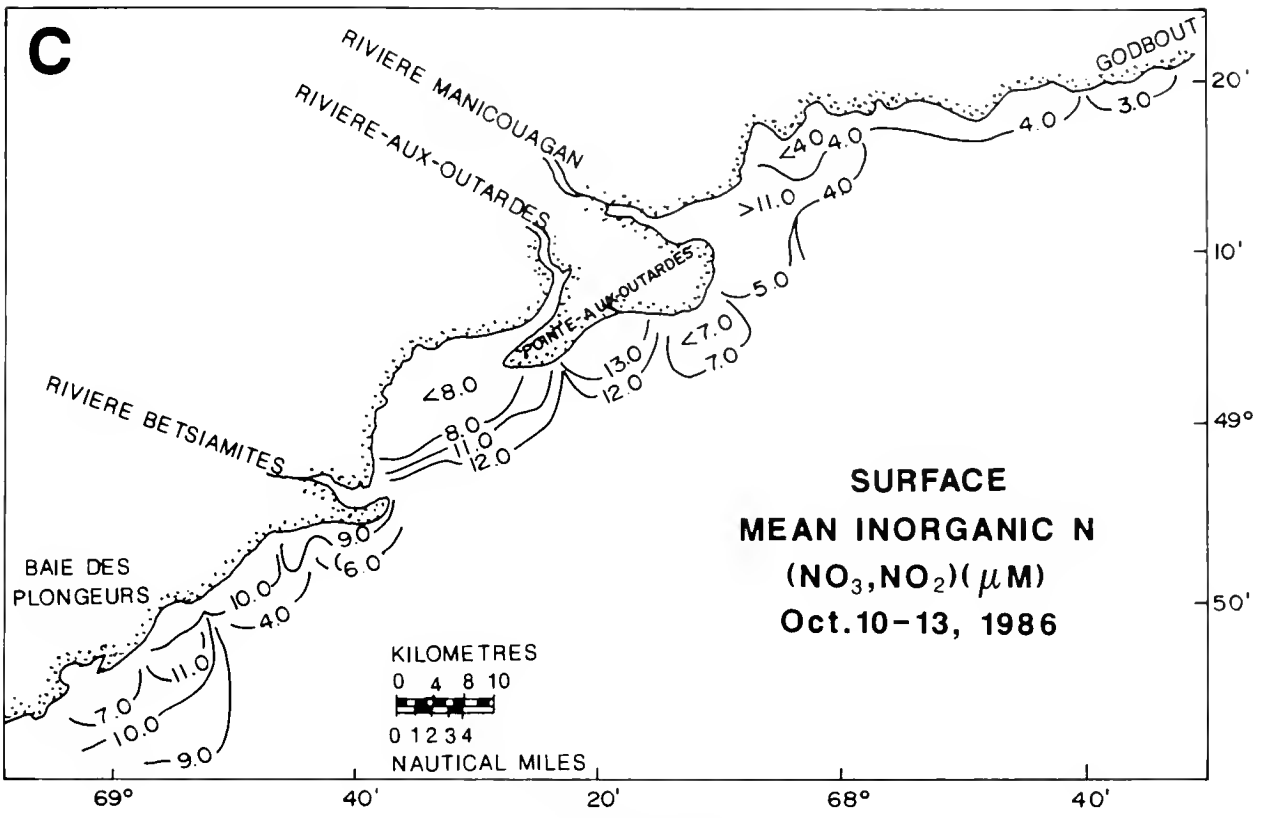


Figure 5 (continued)

levels of C and N in the sediments in October were similarly inconclusive (Figure 7). There was a definite tendency for the greatest accumulation of cysts to occur at intermediate water depths along the plateau (at 80–110 m). However, the % total C and % total N for stations with substantial cyst numbers appeared to vary randomly within a rather limited range.

The relationship between the spatial distribution of cysts in October and paralytic shellfish toxicity in shoreline molluscs was more evident. The two stations identified with the highest PSP toxicity, Franquelin and Grande Baie St-Nicolas (Cembella et al. 1988), also yielded the greatest numbers of *Protogonyaulax* cysts in autumn. When all the stations were considered, the annual mean toxicity level (computed weekly) in *Mya arenaria* was positively correlated ($r = 0.62$, $p \leq 0.05$, n = 11) with the abundance of cysts at adjacent stations (Figure 8). An identical correlation ($r = 0.62$, $p \leq 0.05$, n = 11) was indicated when mean toxicity levels were compared only for the period immediately preceeding and during the autumn cyst sampling period (September 1–October 15). However, there was no significant correlation ($p \leq 0.05$, n = 11) between cyst numbers and *maximum* PSP toxin levels, neither when computed annually ($r = 0.48$), nor only for the period September 1–October 15 ($r = 0.45$).

The zone between the outflow of the Manicouagan and Aux-Outardes rivers corresponded spatially with a peak in shellfish toxicity in early autumn (Figure 9). Lower surface water temperatures, higher salinity (Figures 5A and B), and elevated autumn levels of shellfish toxicity were also asso-

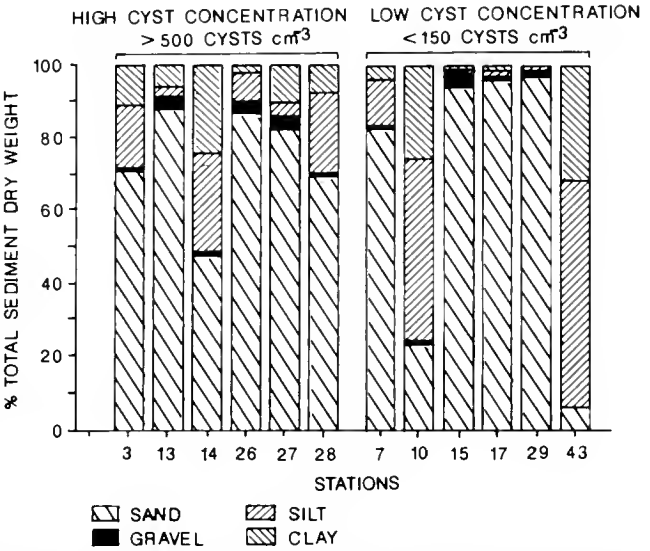


Figure 6. Granulometric analysis of surface sediments (0–5 cm) from selected stations representing extremes of high versus low *Protogonyaulax* cyst concentrations.

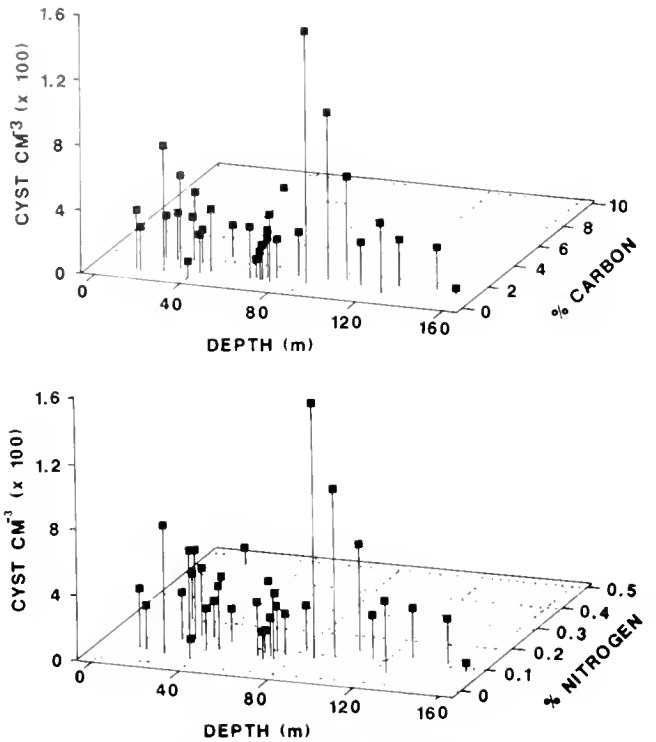


Figure 7. Three-dimensional plots of % total carbon and % total nitrogen in surface sediments versus water column depth and *Protogonyaulax* cyst concentrations.

ciated with the coastal area off Baie des Plongeurs, a region identified as subject to upwelling activity (Therriault and Levasseur 1985, Gratton et al. 1988).

DISCUSSION

The present study represents, to our knowledge, the first definitive report of resting cysts assignable to *Protogonyaulax tamarensis* (Lebour) Taylor (1979) from the St. Lawrence ecosystem. Unfortunately, the taxonomy of the *Protogonyaulax tamarensis/catenella* species complex is currently in dispute (Taylor 1979, 1985, Balech 1985, Loeblich and Loeblich 1979). Due to general conservatism of form and the relative lack of distinctive features among the cysts of members of this species complex (Fukuyo 1985), the difficulties involved in distinguishing morphological variants among motile vegetative cells are further compounded when their respective cysts are considered. It is likely that cysts identified by various authors as those of *Gonyaulax tamarensis* Lebour (1925), *G. tamarensis* var. *excavata* (Braarud) *sensu* Loeblich and Loeblich (1979), *G. tamarensis* var. *tamarensis* (Braarud) *sensu* Loeblich and Loeblich (1979), *G. excavata* (Braarud) Balech (1971), *G. excavata* (Balech) *sensu* Loeblich and Loeblich (1975) and *Protogonyaulax tamarensis* (Lebour) Taylor (1979), represent conspecific, if not synonymous, taxa.

The accumulation of substantial quantities of dinoflagellate cysts in the sediments requires that the depositional rate exceed the rate of loss through regeneration, excystment and dispersive transport. Cyst accumulation would be further optimized by high production ("blooms") of motile cyst-forming species in surface waters. Favorable hydrodynamics, particularly a stratified water column with relatively weak transverse currents during the bloom period, and downward convergences, gyres or shoreward tidal transport, which could concentrate the cysts produced at the termination of the bloom, would also tend to increase cyst deposition. Finally, a fine-grained bottom substrate, preferably with depressions would serve to retain cysts in the sediments.

It is instructive to consider which of these factors could account for the high concentrations of *Protogonyaulax* cysts found in autumn at certain stations adjacent to the Manicouagan peninsula, and at the downstream extent of the freshwater plume. The combined outflow of the Manicouagan/Aux-Outardes river system produces a frontal zone extending into the main body of the Lower estuary (Therriault et al. 1985, Therriault and Levasseur 1985, 1986). High phytoplankton production, particularly of dinoflagellates, has been typically associated with the extent of this plume (Therriault et al. 1985, Cembella and Therriault 1988a, b). For example, the highest cell densities of motile *P. tamarensis* recorded in late summer, the peak bloom period for this species, in both 1980 (Therriault et al. 1985) and 1986 (Cembella and Therriault 1988a, b) coincided with the plume-dominated region of the Lower estuary. This stabilizing outflow of typically warmer, lower salinity water forms part of an estuarine gyre system, as has been repeatedly observed by satellite thermography (Lacroix et al. 1985, Lavoie et al. 1985). The resultant temperature discontinuity has been confirmed for the summer and autumn of 1986 in a time-series of thermographic images (NOAA-7) of surface water temperature which included the Manicouagan/Aux Outardes plume region (Gratton et al. 1988).

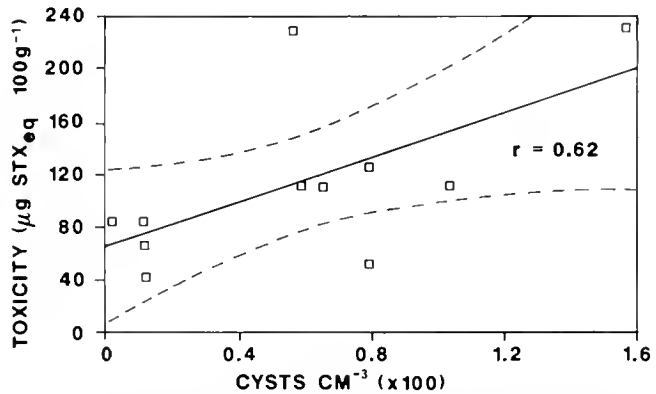


Figure 8. Fitted linear correlation (Pearson correlation coefficient, $r = 0.62$, $p \leq 0.05$) and 95% confidence interval of mean annual paralytic shellfish toxicity in the soft-shell clam, *Mya arenaria*, and *Protogonyaulax* cyst concentrations in surface sediments at adjacent stations during October 1986.

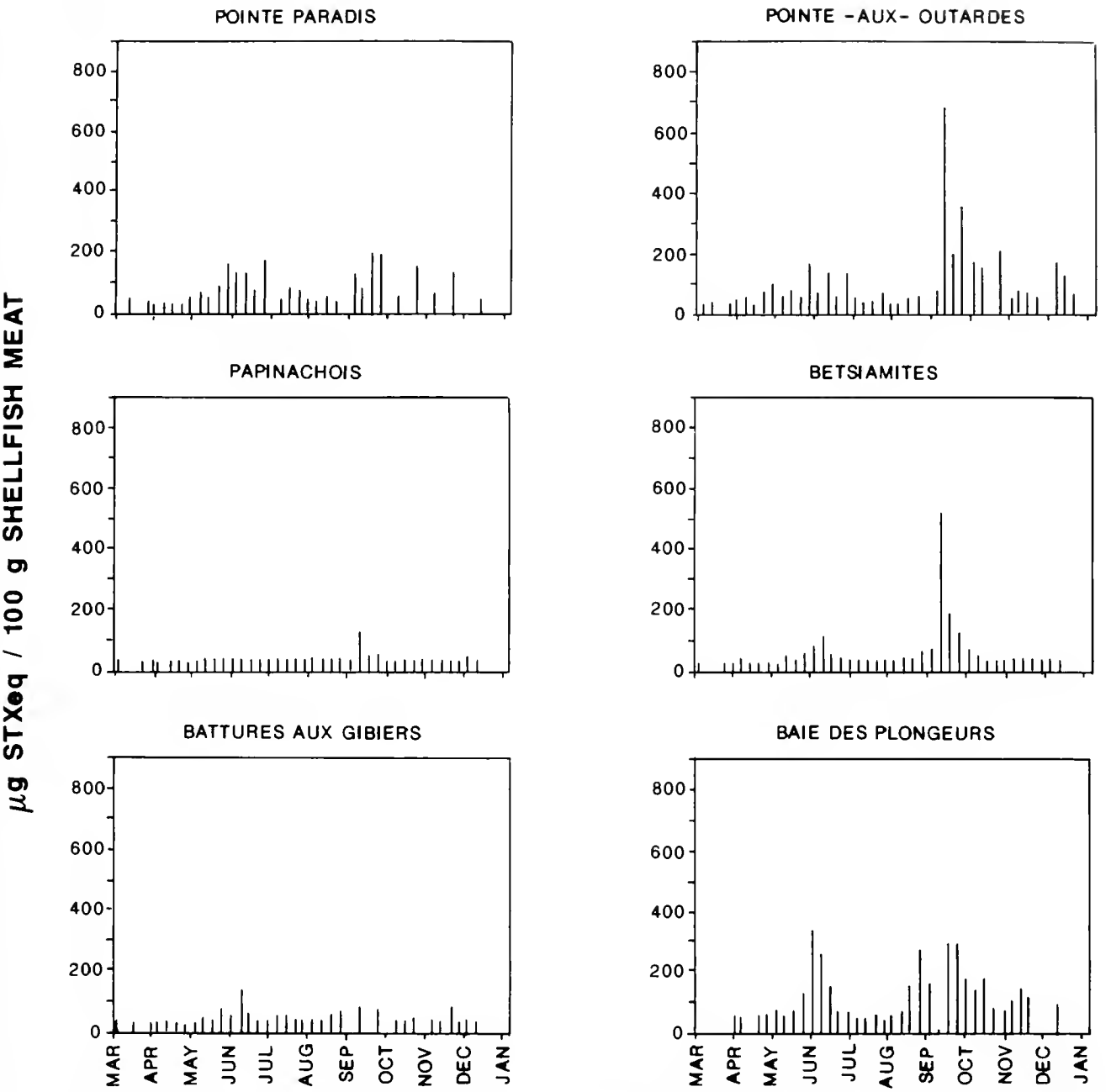


Figure 9. Seasonal variation in paralytic shellfish toxicity of the meat of soft-shelled clams, *Mya arenaria*, at shoreline stations within and adjacent to the zones of river plume influence.

In late August and early September 1986, the frontal zone was frequently visible to the naked eye as sharply delineated longitudinal accumulations of white foam and surface water discolorations offshore from the Manicouagan peninsula (Cembella and Therriault 1988b).

Several lines of circumstantial evidence support the hypothesis that there was a high turnover in the cyst population from year to year in this dynamic frontal area. First, the cysts sampled in October appeared to be relatively "fresh", with morphological and ultrastructural characteristics which corresponded closely with the description of recently formed cysts (Yentsch et al. 1980), rather than mature cysts deposited during previous years. Second, the fact that the % total C in surface sediments was relatively low, and that the dominant sediment grain-size was rather large, strongly suggests a highly dynamic sediment-water interface. In more protected coastal inlets, dinoflagellate cysts numbers have been shown to be positively correlated with % total C in the sediments, as carbon content served as a crude index of organic accumulation, including phytoplankton (Dobell 1976). Third, the relatively low numbers of cysts found in the north shore sediments in June, com-

pared to October, could indicate that the summer blooms resulted from excystment of the overwhelming majority of dormant cysts deposited locally from the blooms of the previous year, leaving few quiescent cysts. However, the low cyst numbers found in summer could also be explained as dispersive loss throughout the previous winter and spring. The active hydrodynamic regime may favor the transport of large numbers of hypnozygotes formed in autumn away from the depositional sites.

Significant observations related to cyst distributions during the pre-bloom period in June 1986 include the low abundance of *Protogonyaulax* in the water column at all north shore stations sampled (Cembella and Therriault 1988b), and the dominance of apparently mature cysts undergoing incipient excystment in the sediments. Intact hypnocysts were rarely found in vertical net tows (30 μm mesh) in the upper 25 m of the water column in June, and none were found routinely in the vertical pump profiles through 50 m depth. However, by mid-July, when the bloom of motile vegetative cells had already been initiated (Cembella and Therriault 1988b), non-motile *Protogonyaulax* cysts were frequently observed in net tows taken near the surface (0–10 m), although not in large numbers.

The above evidence begs the question of whether blooms occurring along the north shore are produced from stable over-wintering *in situ* cyst populations, or from cysts and/or motile cells injected into the water column from elsewhere. Since the presence of winter and early spring cyst populations has not yet been confirmed for the northern shore, this question remains open. The low recovery of hypnocysts in the early summer net tow and pump profiles cannot be used as support against the *in situ* excystment hypothesis, since this sampling was restricted to the upper 50 m of the water column. It is plausible that if these cysts had been resuspended in deeper waters prior to excystment, they would have remained largely undetected by this sampling regime.

The use of a 5 cm sediment depth interval sub-core for cyst enumeration can be justified by the fact that in other coastal ecosystems studied, the majority of dinoflagellate cysts were found to occur in the upper 5 cm of sediment (Anderson et al. 1982, Tyler et al. 1982, White and Lewis 1982), although not necessarily in the surface organic flocculant layer. Considered as passive particles, *Protogonyaulax* cysts are more buoyant than similar-sized inorganic sediment particles, and thus should tend to form superficial layers. When present in deeper sediment layers, buried dinoflagellate cysts, although probably viable, may contribute little to bloom initiation, due to anoxia and other inhibitory micro-environmental factors (Anderson 1984, Anderson and Keafer 1985, Yentsch et al. 1986), unless the sediments are subjected to catastrophic disruption (e.g., through dredging activities).

In agreement with the present granulometric analysis, Robert (1979) also noted a dominance of fine sand in the Pointe-aux-Outardes region, and the general lack of clay in sediments from the lower estuary. Several authors (Dale 1979, White and Lewis 1982, Balch et al. 1983, Schrey et al. 1984, Anderson and Keafer 1985) have mentioned that dinoflagellate cysts are more often associated with the fine-grained sediment fraction, as opposed to sand and gravel. Dale (1976) concluded that the correlation of dinoflagellate cysts with silt particles in Trondheimsfjord, Norway, was evidence that the cysts behaved as fine silt. Along the north shore of the Lower St. Lawrence estuary, the association of highest cyst numbers with sediments dominated by fine-sand tends to indicate that granulometry plays a less significant role in the accumulation of *Protogonyaulax* cysts, than direct physical displacement processes. Perhaps for this reason, cysts were not found to be abundant in the Laurentian Channel transect, although silt concentrations at these stations were the highest observed. In any case, since sandy substrates are relatively poor for retaining deposited cysts, the cyst counts obtained in the present study along the north shore may seriously under-represent the actual numbers arriving at the sediments following bloom senescence.

The nearshore area around the Manicouagan peninsula is known to have the lowest species diversity and lowest benthic faunal biomass in the entire estuary (Robert 1979). This would tend to minimize bioturbation as a mechanism for regeneration of cysts from deeper sediment layers to the surface. The lack of substantial faunal biomass and the low cyst numbers in deeper sediment layers (>5 cm) offers further evidence of active hydrodynamic processes at the sediment/water interface.

Although the mean annual discharge of the St. Lawrence (10.4×10^3 m^3 s^{-1}) and Saquenay (1.3×10^3 m^3 s^{-1}) rivers is large in comparison to the discharge of the Betsiamites, Manicouagan, and Aux-Outardes river systems (data from Environnement Québec), the influence of the latter systems is a strong controlling factor in the plume region. This is due to the isolating effects of the estuarine gyre on the surface circulation, and the proximity of the freshwater discharge source, where the output enters the estuary essentially undiluted. Since outflow is effectively regulated by major dams on each of these rivers, the discharge volume, with the Manicouagan River exerting a dominant influence (Figure 4), is not directly related to precipitation levels, but, rather, reflects the demand for hydroelectric power.

The surface current pattern along the north shore (as indicated in Figure 1) shows a coastal current flowing roughly parallel to the coast in the plume region, then tending to produce a cross-channel circulation toward the south shore at a moderate velocity (El-Sabh 1979, Koutitonsky and El-Sabh 1985). This trans-estuarine flow becomes part of a clockwise gyre, which flows upstream, while a stronger downstream residual current is evident close to the southern shore (El-Sabh 1979). In this context, it is significant that the corresponding southern shoreline,

at least the section between Rimouski and Matane, where the longshore Gaspé current may attain 20 cms^{-1}, is relatively impoverished in *Protogonyaulax* cysts (0–250 cysts cm^{-3}), compared with the northern shore (Cembella and Turgeon, unpublished observations).

According to Koutitonsky and El-Sabh (1985), the bottom circulation in the lower estuary shows a net upstream water displacement toward the plume region, but the current speed is approximately an order of magnitude less than at the surface. If anything, this would tend to concentrate benthic cysts along the northern coastal plateau.

By mid-October, motile *Protogonyaulax* cells had been essentially absent from the upper 50 metres of the water column for at least three weeks (Cembella and Therriault 1988b). Based upon calculations of passive sinking rate of *P. tamarensis* cysts (9.5 m d^{-1}, Anderson et al. 1985), the time between the disappearance of motile *Protogonyaulax* cells from the upper water column and the autumn cyst sampling should have been sufficient to allow for the sedimentation of any cysts formed at the end of the late-summer bloom. Obviously, this time-scale is only valid if vertical mixing and resuspension is assumed to be moderate.

A previous detailed survey in the region of Cape Cod, Mass. revealed a good spatial correlation between shellfish toxicity and the presence of *Protogonyaulax* hypnocysts in the adjacent sediments (Anderson and Morel 1979). In Massachusetts, shallow coastal embayments with limited tidal exchange appear to be functioning as discrete point-sources for bloom formation. There was also an apparent relationship between high cyst numbers and elevated levels of PSP in shoreline molluscs along the north shore of the St. Lawrence estuary, particularly in areas most directly under the influence of the Manicouagan/Aux-Outardes river plume. The two points lying outside the 95% confidence interval in the correlation analysis (Figure 8) both represented stations located beyond the extent of the plume, in zones subject to strong tidal flux. Cyst abundance appeared to track baseline levels of shellfish toxicity more closely, than peaks in toxin load. Nevertheless, even within the plume, the correlation was not sufficiently strong to serve as a predictive index for future shellfish toxicity. A strong correlation between cyst numbers and shellfish toxicity is not necessarily expected in highly dynamic coastal and estuarine areas subjected to excessive tidal mixing and unstable frontal boundaries. Along the coast of Maine, similar attempts to link cyst numbers and shellfish toxicity, as part of a routine monitoring program, have also failed to establish a close causal relationship (Thayer et al. 1983, Yentsch et al. 1986, Shumway et al. 1988).

The high cyst densities found in autumn in the north shore sediments suggest that this area could serve as a cyst reservoir for the entire lower estuary. Through entrainment and trans-estuarine transport, this may result in the contamination of molluscs far from the point-source of cyst origin, perhaps including those from the Gaspé coast. Further studies are in progress to clearly demonstrate whether *Protogonyaulax* blooms in the lower estuary are derived primarily or exclusively from cyst deposits along the northern shore, or whether deep water accumulations from the Laurentian channel, or from along the Gaspé coast, may also contribute substantially to this phenomenon.

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TOXICITY OF CULTURED ISOLATES AND NATURAL POPULATIONS OF *PROTOGONYAULAX TAMARENSIS* FROM THE ST. LAWRENCE ESTUARY

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ABSTRACT The occurrence of paralytic shellfish poisons in shellfish from the lower St. Lawrence estuary has been associated with the presence of the toxic marine dinoflagellate *Protogonyaulax tamarensis* (Lebour) Taylor. Net samples of mixed phytoplankton assemblages within which *P. tamarensis* was dominant were collected from stations on both the north and south coast of the lower estuary. The toxin levels of these natural assemblages were compared with those of unialgal cultured *Protogonyaulax* isolates from the region, by means of the conventional mouse bioassay. In general, although there was considerable unexplained variation, toxin levels from natural assemblages were substantially higher than those from cultured isolates grown under standard conditions. On a per cell basis, toxicity of the natural *Protogonyaulax* populations was among the highest even reported for this species. These highly toxic *Protogonyaulax* from the St. Lawrence estuary may form a cluster with other high toxicity populations from New Brunswick, Newfoundland and the northeastern United States. Under conditions which favor *Protogonyaulax* bloom formation, shellfish in the St. Lawrence region may become rapidly and dangerously toxified by even moderate concentrations of this species in the water column. This poses severe problems for shellfish management in this ecosystem.

KEY WORDS: Paralytic shellfish poisoning, red tide, *Protogonyaulax*, *Gonyaulax*, toxic dinoflagellates, mouse bioassay, saxitoxin

INTRODUCTION

The first reported instances of paralytic shellfish poisoning (PSP) in eastern Canada occurred a century ago (Ganong 1889, Stafford 1912). However, it was not until the late 1940's that *Protogonyaulax* (= *Gonyaulax*) *tamarensis* was proposed as the source of shellfish toxicity in this region (Medcof et al. 1947, Needler 1949). This preliminary conclusion was based upon observations of coincident increase in shellfish toxicity and abundance of *P. tamarensis* in the water column of the Bay of Fundy. The identification of this dinoflagellate as the PSP-causing organism was confirmed by Lebour (1925), who had originally described the species (as *Gonyaulax tamarensis*) from the Tamar estuary near Plymouth, U.K. At the time, *P. tamarensis* had not been associated with shellfish toxicity in southern England. Nevertheless, experiments on natural populations and on cultured isolates eventually confirmed that *P. tamarensis* was the source of PSP in the Bay of Fundy and the Gulf of St. Lawrence (Prakash 1963, 1967, Prakash et al. 1971, White and Maranda 1978, White 1986).

Attempts to revise the nomenclature and to discriminate stable differences in morphology and toxicity among variants of this dinoflagellate which exist along the Atlantic coast of North America have proven to be difficult and controversial (Braarud 1945, Loeblich and Loeblich 1975, Schmidt and Loeblich 1979a, b, Taylor 1984, Balech 1985). Three primary characteristics (toxicity, bioluminescence, and the presence of a ventral pore) used to differentiate among east coast populations were found to occur in a variety of combinations (Schmidt and Loeblich 1979b).

In recent years, the organism responsible for PSP in eastern Canada has often been referred to as *Gonyaulax excavata* (Loeblich and Loeblich 1975, White 1978, 1986, White and Maranda 1978, White and White 1985). This is in accordance with the redescription (Loeblich and Loeblich 1975) of *G. excavata* (Braarud) Balech, as a toxic bioluminescent species lacking a ventral pore on the 1′ epithecal plate. Unlike the revised description of *G. excavata*, as applied to the PSP-causing dinoflagellate from the Bay of Fundy, Gulf of Maine and some New England populations (Loeblich and Loeblich 1975), the St. Lawrence morphotype possesses the distinctive 1′ ventral pore, and produces no apparent bioluminescence in culture. One prominent dinoflagellate taxonomist (Balech 1985) has recognized the Bay of Fundy variant as a new species, *Alexandrium fundyense*, which he distinguished from 'excavata' largely by the absence of this ventral pore. While readily acknowledging the likelihood of genetically distinct intraspecific variants, the present authors tentatively include the St. Lawrence form and the above 'morphospecies' within *Protogonyaulax tamarensis* (Lebour) Taylor (1979).

There is abundant evidence that *P. tamarensis* popula-

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tions can differ in toxicity, particularly among geographically distinct regions (Oshima et al. 1982a, Maranda et al. 1985, Cembella et al. 1987). Toxin content of populations within the same general geographical area sometimes varies as well (Yentsch et al. 1978, Alam et al. 1979, Maranda et al. 1985). *Protogonyaulax* isolates may exhibit strain-specific differences in the spectrum of PSP toxins ('gonyautoxins') produced, even when they are grown under identical conditions (Alam et al. 1979, Shimizu 1979, Hall 1982, Oshima et al. 1982a, Boyer et al. 1986, Cembella and Taylor 1985, Cembella et al. 1987). Since the toxins vary widely in specific toxicity, this may have a dramatic impact on the total toxicity expressed on a per cell basis. The implications of toxin variation, in terms of shellfish toxicity monitoring programs and PSP risk assessment, are three-fold:

1. High numbers of low toxicity *Protogonyaulax* in the water column may prove to be relatively innocuous with respect to shellfish intoxication,
2. As a corollary, even low cell concentrations of high toxicity *Protogonyaulax* may be sufficient to cause dangerous levels of shellfish toxicity,
3. In dynamic environments, such as the St. Lawrence estuary, where blooms tend to be emphemeral and readily dispersed, high toxin levels on a per cell basis may nevertheless result in rapid shellfish contamination.

Although reasonably complete historical records of toxic outbreaks are available for the lower St. Lawrence estuary and the Gaspé coast, and an active shellfish toxicity monitoring program is maintained, only recently has significant attention been focused specifically on the population dynamics of the causative organism (Therriault et al. 1985, Cembella and Therriault 1988, Cembella et al. 1988b). At present, little is known regarding the general physiology and toxicity of *Protogonyaulax* populations in the estuary. It is therefore essential to establish baseline toxin levels for natural *Protogonyaulax* populations indigenous to the St. Lawrence and for cultured isolates, and to compare toxicity with isolates and natural populations from other environments. If environmental and genetic factors which can induce changes in toxicity can be identified within different ecosystems, valuable insight may be gained into the mechanisms of toxin production.

MATERIALS AND METHODS

Collection of Protogonyaulax *from Natural Populations*

During the period May to October 1986, *Protogonyaulax tamarensis* was found on occasion to be the dominant phytoplankton species occurring in the St. Lawrence estuary, both along the section of the north shore which is strongly influenced by the Manicouagan-Aux Outardes river plume, and also on the south coast, near Rimouski (Figure 1). Approximately 1 l of concentrated plankton from natural phytoplankton patches containing *Protogonyaulax* was collected by repeated vertical net tows (30 μm Nitex) for toxin analysis at each station. Net tow samples were examined briefly by phase-contrast microscopy, to gain an impression of the species composition, and to estimate the relative abundance of *Protogonyaulax*. If the *Protogonyaulax* cell density in the net tows was sufficiently high ($\sim 10^4 - 10^5$ cells ml^{-1}), the sample was size-fractionated by passing it through a series of Nitex nets of progressively decreasing mesh size (150, 73, and 20 μm) mounted in PVC cylinders. At each stage, the cells on the net surface were thoroughly rinsed by a gentle stream of ice-cold filtered seawater. The size fraction retained on the 20 μm netting was gently rinsed from the net, decanted into a plastic container, and suspended in cold filtered seawater.

Cell numbers of *Protogonyaulax* and other species in the concentrated 20 μm size fraction were determined immediately on shipboard, or later, in the laboratory, from samples preserved in acidified Lugol's iodine solution. Replicate samples were counted by phase-contrast microscopy in a Palmer-Maloney chamber at 200× magnification. The concentrated sample was stored in the refrigerator (4°C) for several hours until processed for toxin extraction.

For each toxin sample, a sufficient volume of concentrated net plankton was filtered across a 20 μm Nitex mesh to yield 2×10^6 *Protogonyaulax* cells. The cells were gently, but thoroughly, washed with deionized H_2O to remove residual salt, then rinsed into a 50 ml centrifuge tube and concentrated by centrifuging for 5 min at 5,000 × g at 4°C). After removal of the supernatant by aspiration, the pellet was suspended in 4 ml of cold deionized H_2O in a 5 ml conical centrifuge tube and recentrifuged. The supernatant was discarded and the pellet was retained for immediate toxin extraction, or stored frozen (−70°C) for later processing.

Culture and Harvest of Protogonyaulax *Isolates*

Unialgal clonal isolates of *Protogonyaulax tamarensis* (Table 1) were isolated from phytoplankton samples from the St. Lawrence estuary (Figure 1) by micropipette and maintained as reference cultures in the St. Lawrence Algal Culture Collection (SLACC) at the [1]Maurice Lamontagne Institute. Experimental cultures were grown in 2.8 l Fernbach flasks on NWSP-7 (Cembella and Taylor 1986), a nutrient enrichment, which was added to filtered (0.45 μm) estuarine seawater (salinity 26‰) obtained from the field laboratory at Pointe-au-Père (Figure 1). The cultures were incubated in a temperature-controlled growth chamber on a 14/10 h light/dark cycle at 16°C, with an irradiance of 120 $\mu Ein\ m^{-2}\ s^{-1}$ provided by cool-white fluorescent lamps.

The cultures were harvested in late exponential growth phase, which was determined by monitoring the increase in *in vivo* fluorescence with time, as described previously (Cembella et al. 1987). At harvest, the cell concentrations were determined by optical microscope counts in replicate

TABLE 1.

Origin of *Protogonyaulax tamarensis* clones isolated from the St. Lawrence estuary (Figure 1).

Isolate No.	Station	Date of sampling
Pr 1a	I	July 15, 1985
Pr 2a	I	July 17, 1985
Pr3a	I	July 21, 1985
Pr 4a	II	July 31, 1985
Pr 5a	VI	July 31, 1985
Pr 6a	I	August 2, 1985
Pr 8f	VII	August 16, 1985
Pr 9a	I	August 23, 1985
Pr 11c	IV	August 23, 1985
Pr 11f	IV	August 23, 1985
Pr 16a	II	September 10, 1985
Pr 17b	III	September 10, 1985
Pr 18b	IV	September 10, 1985
Pr 19a	V	September 12, 1985
Pr 20c	VI	September 12, 1985

Palmer-Maloney counting chambers. Cells were collected upon 20 μm Nitex screens and prepared for toxin extraction according to the same protocol as for the natural populations. The loss of cells through the 20 μm net was estimated by microscopic examination of the filtrate, and was always found to be negligible.

Extraction and Bioassay of Toxins

The procedure adopted for the extraction of toxins from *Protogonyaulax* was a modification of the standard AOAC (1984) method for the preparation of toxic shellfish samples for mouse bioassay. The cell pellets contained in 5 ml conical plastic centrifuge tubes were suspended in 3 ml 0.1 N HCl, then probe-sonicated (3 min. at 75 W output) to release the toxins. Microscopic examination (400×) of cell debris remaining after sonication revealed that the cells had been completely disrupted. The cell suspension was transferred to a 20 ml glass scintillation vial, and a further 2 ml of 0.1 N HCl were added. The vial was heated for sufficient time on an aluminum hot block to boil the liquid extract for 5 min. After cooling the vial to room temperature, the pH was carefully adjusted to 3.4–3.6, and the total volume of extract was measured. The extract was centrifuged for 10 min. at 10,000 × g, then the supernatant volume was adjusted to 20 ml with deionized H_2O and submitted for mouse bioassay (Microbial Hazards Division, Dept. of Health and Welfare, Ottawa).

Mouse bioassays were performed according to the AOAC (1984) method, by injecting six female (20 g) mice per assay. The bioassays were calibrated using reference saxitoxin (STX) standard obtained from the Division of Microbiology, Food and Drug Administration, 1090 Tusculum Ave., Cincinnati, OH. Toxin levels in μMouse Units, as determined by death time, were converted to saxitoxin equivalents (STXeq) using the conversion factor: 1 Mouse Unit = 0.215 STXeq.

RESULTS

At the time the natural plankton samples were collected for toxicity analysis, *Protogonyaulax tamarensis* (Figure 2) was overwhelmingly the dominant phytoplankton species in the net tows. However, cursory qualitative examination of the net samples revealed that other microplankton (<150 μm) species, especially chain forming diatoms, including *Chaetoceros* and *Thalassiosira* spp., and rotifers, were also common at most stations. By passing the net samples through the 150 μm and 73 μm screens, the percentage of *Protogonyaulax* was further increased (Table 2). This left only some fragments of diatom chains, a few cells of other dinoflagellates species, and sometimes a minor presence of tintinnids as 'contaminants' in the samples for toxin extraction. The tintinnid component consisted principally of *Helicostomella* sp. and *Tintinnopsis* spp. The latter species were often observed with intact or partially digested *Protogonyaulax* cells in the digestive cavity.

During the period when *Protogonyaulax* constituted a high proportion of the phytoplankton assemblage in net tows at stations along the north shore, surface water temperatures varied between 6.8–10.9°C and ambient inorganic phosphate levels were 0.76–1.13 μg at l^{-1}. Examination of the seasonal variation in shellfish toxicity in the soft-shelled clam, *Mya arenaria*, at two stations on the north shore adjacent to those sampled for *Protogonyaulax* (Figure 3) indicated that toxin levels began to rise while the relative percentage of *Protogonyaulax* in the water column was high. However, peak toxicity in shoreline molluscs did not occur until this toxic dinoflagellate was no longer observed in surface net tows.

According to the mouse bioassay, the toxin levels of both natural *Protogonyaulax tamarensis* populations (78.8 ± 11.7 SE pg STXeq $cell^{-1}$, n = 9) and cultured isolates (32.8 ± 7.8 SE pg STXeq $cell^{-1}$, n = 15) from the St. Lawrence estuary were consistently high (Figure 4). Comparison of the toxicity of cultured St. Lawrence isolates with those from diverse locations (Table 3), revealed that the St. Lawrence group would rank among the most toxic.

Two isolates were sub-cultured and the cells were harvested for toxin measurements from three successive transfer series. The variation in toxicity for isolates Pr 6a (7.4 ± 1.0 SE, n = 3) and Pr 16a (18.0 ± 1.7 SE, n = 3), which could be attributable to the failure to duplicate culture, harvest, and bioassay conditions identically, was judged to be of low significance.

A non-parametric Mann-Whitney U-test was applied to test for the significance of the difference in mean toxicity between the cultured isolates and natural populations from the St. Lawrence. The results indicated that cells from natural populations were significantly more toxic than cultured isolates ($P < 0.001$). Microscopic measurements of indi-

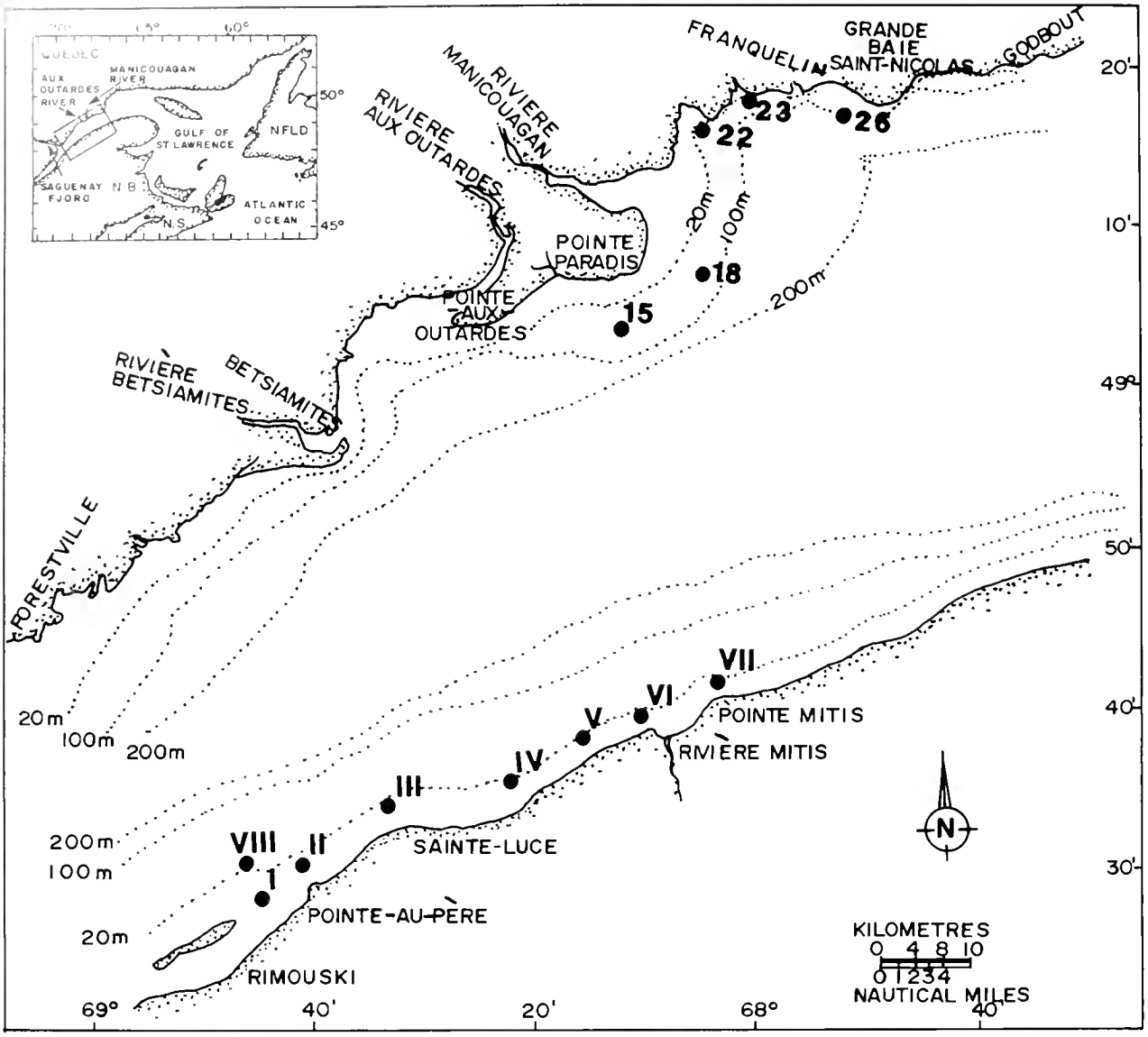

Figure 1. Location of sampling stations in the lower St. Lawrence estuary for natural *Protogonyaulax* populations and the isolation of clones in culture.

vidual cells using an optical micrometer, showed that differences in cell volume between these two groups were not significant, and could not account for the observed higher toxicity, on a per cell basis, in natural populations.

DISCUSSION

The use of the conventional mouse bioassay to measure toxicity of *Protogonyaulax* from natural phytoplankton samples is limited to the determination of 'non-specific' total toxicity. The presence of other toxic plankton in bioassay samples could produce an enhanced or synergistic toxic response, which might be interpreted as elevated levels of PSP toxins alone. In the present study, phytoplankton samples from the St. Lawrence estuary contained the dinoflagellate *Dinophysis acuminata* (Table 2), a known cause of diarrhetic shellfish poisoning (DSP) (Kat 1985). However, even given the possibility that mouse bioassay symptoms of DSP could be misdiagnosed as those of PSP, *D. acuminata* was not present in numbers sufficient to result in any significant enhanced toxic effect. Furthermore, DSP toxins are considered to be labile under the acid extraction and heat treatment specified by the AOAC (1984) protocol for the preparation of PSP toxin extracts (T. Yasumoto pers. comm.).

The higher toxin levels in the natural populations cannot be accounted for by assuming a contribution to total toxicity due to *Protogonyaulax* cells ingested by zooplankton predators. With the exception of the sample from ST VIII, where the tintinnid *Helicostomella* sp. was relatively numerous, such predators were rare in the 20 μm net fraction.

Figure 2. Light micrograph (Mag. 400×) of *Protogonyaulax tamarensis*, the dinoflagellate responsible of paralytic shellfish poisoning in the St. Lawrence estuary.

Since the duration of the bloom period for *Protogonyaulax* at the stations monitored was limited to a few weeks in late summer, and the blooms were found to aggregate in readily dispersed 'patches', the opportunities for time series sampling at particular stations was severely restricted. This limitation on the number and frequency of stations sampled did not permit us to establish spatio-temporal correlations with toxin content, nor associations between toxicity and specific environmental factors. More detailed study is required to evaluate the relative contributions of environmental and genetic effects, to account for the four-fold variation in toxicity per cell observed among the natural populations.

In culture, where the environmental effects on toxicity can be more closely controlled, the high degree of interclonal variation in toxicity among the St. Lawrence isolates was nonetheless rather remarkable. This variation was observed even among cultures harvested at the same point of the growth curve, during late exponential phase, when toxin levels were typically at maximum. On the other hand, for a given isolate harvested at that same time in the culture cycle, toxin levels were rather conservative. Since all of the isolates were grown under identical conditions, the observed differences in toxicity among isolates presumably have a genetic basis. This could be reflected in distinct toxin spectra, or in differences in metabolic capacity to selectively produce and store the toxins. Preliminary evidence from toxin profiles of three St. Lawrence isolates (Pr 1a, Pr 2a, Pr 3a) analyzed by high-performance liquid chromatography, revealed that the dominant toxins present in extracts treated with hot 0.1 N HCl (AOAC 1984) were similar on a percent molar basis (gonyautoxin 2 = 6.8–17.7%, gonyautoxin 3 = 51.0–63.5%, neosaxitoxin = 27.7–28.0%, saxitoxin = 2.1–3.3%), but total toxin content varied quantitatively among these isolates (Cembella et al. in prep.).

In view of the problems faced by classical morphological taxonomists in discriminating species, and given the potential for genetic isolation of populations from the St. Lawrence estuary, such biochemical information on toxicity and toxin composition is highly significant. An evolutionary interpretation of high toxicity northern *Protogonyaulax* variants would presume the adaptive evolution of ecotypes, physiological races, varieties (in the botanical sense), or possibly sibling species. On the basis of enzyme electrophoretic data, toxin composition and nuclear DNA evidence, the existence of such biochemically distinct variants within the genus *Protogonyaulax* has been previously postulated (Cembella and Taylor 1985, 1986, Cembella et al. 1987, 1988a).

Unfortunately, the number of studies of toxicity in natural *Protogonyaulax* populations in the literature is insufficient to identify specific environmental factors or environmental gradients which could be linked to higher toxin production. Nevertheless, the present evidence of high toxicity for St. Lawrence estuary isolates and natural populations further supports the proposed existence of a clinal gradient of increasing toxicity per cell progressing from south to north along the eastern coast of North America (Maranda et al. 1985, Cembella and Therriault, 1988). The St. Lawrence populations appear to represent a more northernly extension of the high toxicity cluster above 43°N latitude (from Cape Cod to the Bay of Fundy).

From an ecological standpoint, there are several possible explanations for the high toxicity found in St. Lawrence populations. First, such populations may be subject to transient or persistent environmental stresses, including salinity or temperature extremes or high turbulence, which could directly affect the metabolic pathways leading to toxin production. Another possibility (which is not mutually exclusive of the first), is that under suboptimal environmental conditions in nature, increased toxicity on a per cell basis may result from a decrease in growth rate. This would occur due to failure of cells to 'dilute' internal high toxin levels through rapid mitosis and cytokinesis. White (1976) showed that *Protogonyaulax* cultures subjected to turbulence exhibited a decrease in growth rate, even if the stress was applied for less than an hour per day. A third possibility is that St. Lawrence populations may differ genetically from their southern counterparts, in ways which allow them to be well adapted to their environment, while maintaining both high toxin levels and a high growth rate. This possibility cannot be discounted, since *in situ* growth rates have not been measured for these natural populations. Either fortuitously, or for unknown reasons linked to their ability to maximize acclimation to the environment, toxin production may be enhanced.

It is interesting to note that the highly toxic *Protogonyaulax* from the St. Lawrence represent the most northern

TABLE 2.

Percent species composition of microplankton (20–73 μm) samples used for toxin extraction.

	ST 15 Sept. 3 1986	ST 15 Sept. 4 1986	ST 18 Aug. 26 1986	ST 18 Sept. 4 1986	ST 22 Aug. 25 1986	ST 23 Aug. 25 1986	ST 26 Aug. 25 1986	ST 1 Sept. 10 1986	ST VIII July 30 1987
Dinoflagellates									
Ceratium fusus	—	—	—	—	—	0.1	—	—	—
Dinophysis acuminata	0.4	0.8	0.8	0.8	1.1	0.8	0.7	0.9	—
Protogonyaulax tamarensis	96.0	97.5	78.2	85.2	89.5	94.5	62.1	98.7	79.6
Protoperidinium depressum	—	—	0.4	—	1.3	1.1	0.4	0.2	0.2
Diatoms									
Nitzschia sp.	—	—	—	—	—	—	—	—	0.9
Skeletonema costatum	1.9	0.4	9.1	6.4	—	—	20.4	—	0.7
Thalassionema nitzschiodes	—	—	5.7	2.0	—	0.9	12.5	—	0.2
Thalassiosira sp.	1.7	1.2	4.4	5.1	0.2	—	0.9	—	3.0
Tintinnids	—	—	1.5	0.5	8.0	2.5	3.2	0.2	15.5
TOTAL	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

population(s) of those compared (Table 3). They exist in a dynamic natural environment, characterized by high levels of tidal and wind mixing, low ambient temperatures, and nutrient concentrations which are rarely, if ever, limiting (Therriault and Levasseur 1985). Isolates from the Bay of Fundy, another highly turbulent northern environment, comparable to the lower St. Lawrence estuary, also exhibited strikingly high toxin levels (White 1986).

White (1978) found that a New England isolate of *P. tamarensis* (referred to as *Gonyaulax excavata* by the author) was more toxic when grown at higher salinity, and he speculated that offshore and coastal populations may be more toxic on a per cell basis than those from estuaries. Yentsch et al. (1978) also noted that 'non-toxic' natural populations from the coast of Maine and an isolate from Plymouth, U.K. were both from 'estuarine' populations, while morphologically similar *Protogonyaulax* found along the exposed Maine coast were found to be toxic. This suggested link between estuarine conditions and low toxicity in *Protogonyaulax* is not in accord with the results of the present study, where the presence of high toxicity *Protogonyaulax* populations during late summer was strongly influenced, if not controlled by, the strong combined freshwater outflow of the Manicougan-Aux Outardes river systems (Therriault and Levasseur 1985, Therriault et al. 1985, Cembella and Therriault unpublished observations). Furthermore, Prakash's (1963, 1967) work on an isolate from the Bay of Fundy, which grew optimally at a low salinity of 19–20‰ (an 'estuarine' clone), was more toxic (maximum toxicity 35.5 pg STXeq cell^{-1}) than the New England isolate assayed by White (1978) (maximum toxicity ~2.5 pg STXeq cell^{-1}), when both were grown at equivalent salinities (~30–31‰).

It is difficult to separate the direct effects of environmental stresses on toxin production from indirect effects resulting in a decrease in growth rate under suboptimal

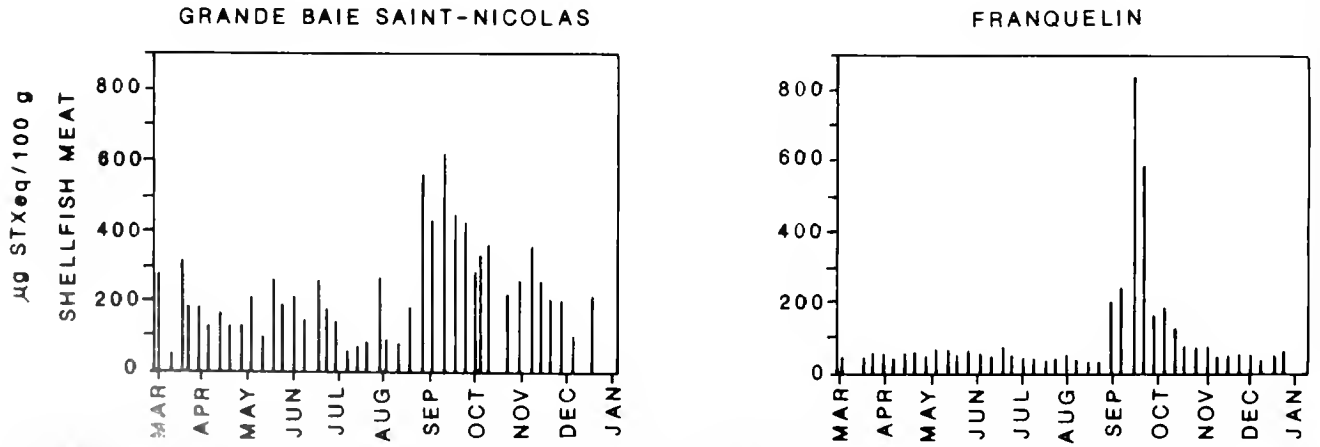

Figure 1. Seasonal variation in PSP toxicity of the meat of the soft-shelled clam, *Mya arenaria*, at two shoreline stations along the north coast of the St. Lawrence estuary in 1986.

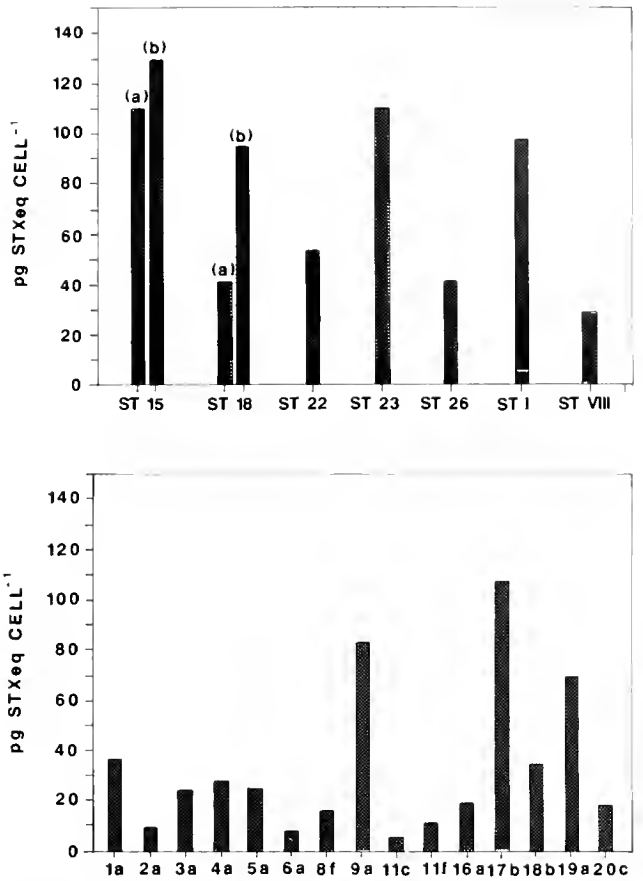

Figure 4. Toxicity of *Protogonyaulax tamarensis* from natural populations and cultured isolates from the St. Lawrence estuary, as determined by mouse bioassay (n = 6). Sampling dates for natural populations: ST 15, (a) Sept. 3, 1986, (b) Sept. 4, 1986; ST 18, (a) Aug. 26, 1986, (b) Sept. 4, 1986; ST 22, Aug. 26, 1986; ST 23, Aug. 26, 1986; ST 26, Aug. 25, 1986; ST I, Sept. 10, 1986; ST VIII, July 30, 1987. For cultured isolates, the code on the X-axis refers to SLACC isolate designations.

conditions. In either case, environmentally induced changes in toxicity appear to occur without markedly affecting the spectrum of toxins produced (Boyer et al. 1985, 1986, 1987, Ogata et al. 1987). The study on St. Lawrence isolates supports the previous contention that natural *Protogonyaulax* populations are more toxic than cultured isolates from the same environment (Kodama et al. 1982, White 1986). Evidence from culture studies (Hall 1982, Boyer et al. 1985, 1987, Ogata et al. 1987) showed that growth at lower temperatures and lower ambient phosphorus levels resulted in an increase in toxicity per cell, and that these elevated toxin levels were relatively independent of changes in cell volume. Although there was no evidence of growth rate limitation by phosphorus in the St. Lawrence estuary during the period when the natural populations were sampled for toxin analysis, both inorganic phosphate concentration and growth temperature employed for the culture of the isolates were markedly elevated over *in situ* levels.

The St. Lawrence isolates grew optimally at a temperature between 15–18°C in culture, but mean ambient surface temperature at the stations on the south coast from July 15–September 12, 1985, the period during which samples were obtained for isolation of *Protogonyaulax* cultures, decreased gradually from a maximum of 15.9–6.5°C. Ambient inorganic-P levels along the southern shore of the estuary fluctuated between 1.0–1.8 μg at P l^{-1} in late summer, although the cultures were grown on 100 μg at P l^{-1} (Cembella and Taylor 1986). This suggests that in seawater media supplemented with high nutrient levels typically used for dinoflagellate culture, 'forced growth' may occur in cultures, particularly in those grown at artificially high temperatures. In view of the possibility that growth rates achieved in culture may not be representative of those in nature, or that the factors controlling growth rate may be completely different, White's (1986) cautionary statement against the extrapolation of toxicities derived from cultures to natural populations is well advised. Toxicity values from cultured isolates should be considered only in relation to those obtained from other cultured isolates, and not as strictly representative of the natural environment. Comparisons of the toxicity of St. Lawrence populations with those from diverse locations as reported in the literature (Table 3) must also be viewed carefully, since culture conditions, growth media, and the point in the growth cycle during which the cells were harvested were not identical.

The above observations on toxin variations lead to the conclusion that simple monitoring of the cell concentrations of 'toxic' dinoflagellate species may be of limited value, without some knowledge of their specific toxicity. Estimates may be made by mouse bioassays, if proper controls are maintained to eliminate toxin 'cross-reactions' with toxic components from other species, but detection can be more accurately done by fluorometric methods (Boyer et al. 1987, Cembella et al. 1987). Toxin levels are subject to environmental factors, clonal variation and experimental error (Maranda et al. 1985, White 1986, Cembella et al. 1987), but the discrepancies are, at worst, several fold, and can still provide a crude basis for comparison among populations from different ecosystems. However, this does point out the need for physiological studies on toxin production of both vegetative cells and cysts from natural populations, as well as on cultured isolates grown under more realistic environmental conditions.

Even though aggregations of *Protogonyaulax* along the north shore of the estuary in the summer of 1986 were neither dense nor persistent enough to be considered a 'red tide', high toxicity on a per cell basis can account for the rapid toxification of shoreline molluscs in the St. Lawrence estuary. Prakash et al. (1971) have previously commented that visible *Protogonyaulax* blooms are not typically observed in the Bay of Fundy and the St. Lawrence region, yet toxic shellfish and illnesses resulting from the consumption of PSP contaminated shellfish have been consis-

TABLE 3.

[1]Toxicity (pgSTXeq cell^{-1}) obtained from literature values for *Protogonyaulax tamarensis* cultured isolates and natural populations.

[2]*Protogonyaulax* Isolate no.	Origin	[9]Toxicity (pgSTXeq cell^{-1}) n_1 = number of replicates n_2 = number of isolates or samples of natural populations	Reference
Cultured Isolates			
North American Atlantic Coast			
[3]Unspecified	Harbour Grace, Newfoundland, Canada	39	White & White 1985
[4]NEPCC 545 (= Isolate #7)	Bay of Fundy, N.B., Canada	[10]22.57 ± 5.66 SD n_1 = 4	Cembella et al. 1987
[3]#1–#7		35.5 ± 3.4 SE n_2 = 10	White 1986 and references cited therein
[5]GtMEM10, GtMEF10, GtME8, GtME6, GtMEM21, GtME20, GtME1	Gulf of Maine, ME	[11]16 ± 4 SE n_2 = 7	Maranda et al. 1985
[5]Unspecified		50	Mickelson & Yentsch 1979
[6]422	Gloucester, MA	7.0 n_1 = 10	Schmidt et al. 1978
[7]422		[11]9.7 ± 0.1 SD n_1 = 10	Schmidt & Loeblich 1979a
[6]423		6.9 n_1 = 10	Schmidt et al. 1978
[6]427		10 n_1 = 10	Schmidt et al. 1978
[6]429 (= UTEX 2165)		11 n_1 = 10	Schmidt et al. 1978
[3]429		3.8 n_1 = 10	White 1978
[5]429		20.5	Alam et al. 1979
[7]429		[11]24 ± 2 SD n_1 = 10	Schmidt & Loeblich 1979a
[7]520	Mill Pond, Orleans, MA	[11]3.8 ± 0.5 SD n_1 = 10	Schmidt & Loeblich 1979a
[5]Unspecified Woods Hole Oceanographic Institute isolate		4.3	Alam et al. 1979
[8]519	Perch Pond, Falmouth, MA	[11]2.8 ± 0.1 SD n_1 = 10	Schmidt & Loeblich 1979a
[5]Unspecified Woods Hole Oceanographic Institute isolate		2.2	Alam et al. 1979
[5]Gtm242, Gtm243, Gtm253, Gtm240B, GtMP, GtMP4, GtMP9, GtMP21, GtMMP103, GtMMP104, GtMMP117, GtCH4, Gt270, GtPPb1, GtPPkF, GtG9B, GtSP1	Massachusetts	[11]9 + 2 SE n_2 = 17	Maranda et al. 1985
[5]GtC, GtCN-1, GtC-2	Groton, CT	[11]1 ± 0 SE n_2 = 3	Maranda et al. 1985
[5]GtLI18-C, GtLI-11, GtLI-15, GtLI12-A, GtLI12-C	New York State	[11]3 ± 1 SE n_2 = 5	Maranda et al. 1985
North American Pacific Coast			
[4]NEPCC 180	Brentwod Bay, B.C., Canada	[10]Trace	Cembella et al. 1987a
[8]NEPCC 71 (= 517)	Patricia Bay, B.C., Canada	[11]0.17 n_1 = 10	Schmidt & Loeblich 1979
[3]NEPCC 71		[10]Trace	Cembella et al. 1987

TABLE 3.

Continued

[2]*Protogonyaulax* Isolate no.	Origin	[9]Toxicity (pgSTXeq cell^{-1}) n_1 = number of replicates n_2 = number of isolates or samples of natural populations	Reference
NEPCC 400-NEPCC 407, NEPCC 409, NEPCC 412, NEPCC 516	English Bay, B.C., Canada	[10]1.32 ± 0.19 SE n_2 = 11	Cembela et al. 1987
[8]NEPCC 255 (= 516)	Lummi Island, WA	[11]2.2 ± 0.4 n_1 = 10	Schmidt & Loeblich 1979a
[4]NEPCC 255		[10]2.1	Boyer et al. 1986
[4]NEPCC 255		[10]4.29 ± 1.77 SD n_1 = 4	Cembella et al. 1987
[8]174 (= FCRG 53)	La Jolla, CA	Undetectable	Schmidt & Loeblich 1979a
Japan			
[4]FK-788	Funka Bay, Hokkaido, Japan	22	Oshima et al. 1982a
[4]OK-794	Okkirai Bay, Iwate Prefecture, Japan	7.5	Oshima et al. 1982a
[4]Unspecified	Ofunato Bay, Iwate Prefecture, Japan	1.30	Kodama et al. 1982
[4]OF84423D-3		24.2	Ogata et al. 1987
[6]OF-1		8.6	Oshima & Yasumoto 1979
[4]OF-776 (= OF-1), OF-793, OF-796, OF-803		6.5 ± 0.4 SE n_2 = 4	Oshima et al. 1982a
[4]OF-776		37	Singh et al. 1982
[4]ORFC-789, Unspecified		7.8 ± 0.9 SE n_2 = 16	Oshima et al. 1982b
[4]KS-796	Kesennuma Bay, Miyagi Prefecture, Japan	7.3	Oshima et al. 1982a
Northern Europe			
[4]NEPCC 183 (= Plymouth 173)	Plymouth, U.K.	[10]Undetectable	Cembella et al. 1987
[8]439 (= Plymouth 173)		Undectable	Schmidt & Loeblich 1979a
[8]440 (= Plymouth 173a)		Trace	Schmidt & Loeblich 1979a
[5]GEXC 9-GEXC 12, GEXC 54, GEXC 56	Ares, Galicia, Spain	21.1 ± 3.1 SE n_2 = 6	Blanco et al. 1985
[5]GEXC 1-GEXC 3, GEXC 6, GEXC 39	La Coruna, Galicia, Spain	Trace n_2 = 5	Blanco et al. 1985
[4]NEPCC 253	Laguna Obidos, Portugal	[10]0.43 ± 0.05 SD n_1 = 4	Cembella et al. 1987
Natural populations			
[4]*Protogonyaulax tamarensis*	Ofunato Bay, Iwate Prefecture, Japan	38.66 ± 2.04 SE n_2 = 9	Kodama et al. 1982
[3]*Gonyaulax excavata*	Bay of Fundy, N.B., Canada	210 ± 50 SE n_2 = 32	White 1986

[1] Considered to be maximum toxicity for cultured isolates, based upon cultures harvested in exponential phase, except for Mickelson & Yentsch 1979 and Oshima et al. 1982a, who assayed cells collected in stationary phase.

[2] Species designations according to or inferred from those given by the original authors. Nomenclatural differences may represent conspecific variants within the species *Protogonyaulax tamarensis* Taylor, and many of the names are synonomous.

[3] *Gonyaulax excavata* (Braarud) Balech *sensu* Loeblich and Loeblich (1975)

[4] *Protogonyaulax tamarensis* (Lebour) Taylor

[5] *Gonyaulax tamarensis* Lebour

[6] *Gonyaulax excavata* (Braarud) Balech

[7] *Gonyaulax tamarensis* var. *excavata sensu* Schmidt and Loeblich (1979b)

[8] *Gonyaulax tamarensis* var. *tamarensis sensu* Schmidt and Loeblich (1979b)

[9] Where necessary, toxicity in pgSTXeq cell^{-1} was calculated from values given in Mouse Units, assuming a conversion factor of 1 Mouse Unit = 0.22 μg STXeq, unless otherwise specified by the authors.

[10] Toxicity determined by HPLC.

[11] Conversion factor: 1 Mouse Unit = 0.18 μgSTXeq.

tently reported from both of these environments. Now, in view of the known high toxicities in natural *Protogonyaulax* populations, and the potential for rapid accumulation of toxins by molluscs, a significant change in the strategy (frequency and spatial covering) of shellfish and toxic bloom monitoring programs may be required for the St. Lawrence and similar dynamic coastal ecosystems.

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A COMPENDIUM OF THE RESPONSES OF BIVALVE MOLLUSCS TO TOXIC DINOFLAGELLATES

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INTRODUCTION

The biology of toxic dinoflagellates, and the threat to public health caused by their presence, have been studied in great detail by a number of workers (see LoCicero 1975, Taylor and Seliger 1979, Anderson et al. 1985). Until recently, however, little attention has been given to the effects of these organisms on their molluscan hosts. A number of authors have, in fact, states that the dinoflagellates have little effect on the host animals (e.g., Prakash et al. 1971, Quayle 1969, Arafiles et al. 1984, Estudillo and Gonzales 1984). Although there are data to the contrary, this belief has prevailed and has been reiterated often in the literature.

In a recent series of papers, Shumway and co-workers have studied the behavioral and physiological responses of bivalve molluscs to the presence of the toxic dinoflagellate, *Protogonyaulax tamarensis*. We have shown that not only are the host organisms affected by the presence of the dinoflagellates, but that the effects are species specific, geographically specific and often dramatic. In this review, we summarize the data on the effects of various species of toxic dinoflagellates on the behavior and physiology of bivalve molluscs.

Shell Valve Closure

Perhaps the most widely reported effects of red tide organisms upon bivalve molluscs is isolation from the environment either by valve closure or reduced filtration. Differential valve closure has been reported in *Brachiodontes recurvis* and *Crassotrea virginica:* valve closure increased in the presence of *Gymnodinium monilata* but was normal in the presence of *G. breve* (Sievers 1969). Differential valve closure has also been reported in *Mytilus edulis* by Shumway and Cucci (1987). While *M. edulis* from Maine showed no response to the addition of *Protogonyaulax tamarensis* (clone GT429), *M. edulis* from Rhode Island showed varying degrees of shell-valve closure when presented with GT429 (Figure 1). While 3 animals were shown to continue normal activity patterns (Figure 1b), the majority (15) exhibited at least partial shell-valve closure. Echalent siphons were closed and the mantle edges in otherwise "open" animals were retracted. Similar patterns of shell-valve activity were noted in Spanish *M. edulis* in the presence of GT429 (Figure 1d, e), Two-thirds of these animals tested showed initial, erratic shell-valve closure followed by complete closure.

Both *Crassostrea virginica* and *Ostrea edulis* remained open in the presence of GT429 (Figure 2). *O. edulis* normally had the shell valves open and the mantle edges were visible. Addition of GT429 caused partial adduction of the shell valves in only four of the 14 animals studied (Figure 2a). Figure 2b shows the typical response of *O. edulis* to the introduction of GT429. There was an initial, partial adduction of the shell valves followed by periodic "snaps." This activity pattern continued until clean sea water was introduced. *C. virginica* exhibited an initial shell-valve closure when GT429 was presented. This closure was followed by a gradual reopening (Figure 2c) and the pattern repeated, although complete closure never occurred. (Shumway and Cucci 1987). Ray and Aldrich (1976) reported that *C. virginica* rarely opened when exposed to *Gonyaulax monilata* (=*Gessnerium monilatum*, Loeblich), but opened frequently in the presence of *Gymnodinium breve* (=*Ptychodiscus brevis*, Steidinger). Dupy and Sparkes (1968) reported valve closure accompanied by vigorous "clapping" of the valves in *C. gigas* upon exposure to *Gonyaulax washingtonensis*.

Placopecten magellanicus showed the most striking behavioral responses of any species studied by Shumway and Cucci (1987). While 2 animals showed no response, the majority (14) exhibited an immediate closure of the shell valves followed by either violent swimming activity, partial, sustained shell-valve closure, or a combination of the two (Figure 3a). Swimming/clapping activity patterns were never observed to last for more than 30 min.–1 hr. On addition of clean sea water, the activity ceased (Figure 3b) and the animals remained open with the mantle edges and tentacles freely exposed.

Spisula solidissima, Modiolus modiolus, Artica islandica and *Guekensia demissa* showed no change in valve activity upon exposure to GT429, while *Mercenaria mercenaria* showed a pronounced valve closure (Figure 3), Shumway and Cucci 1987).

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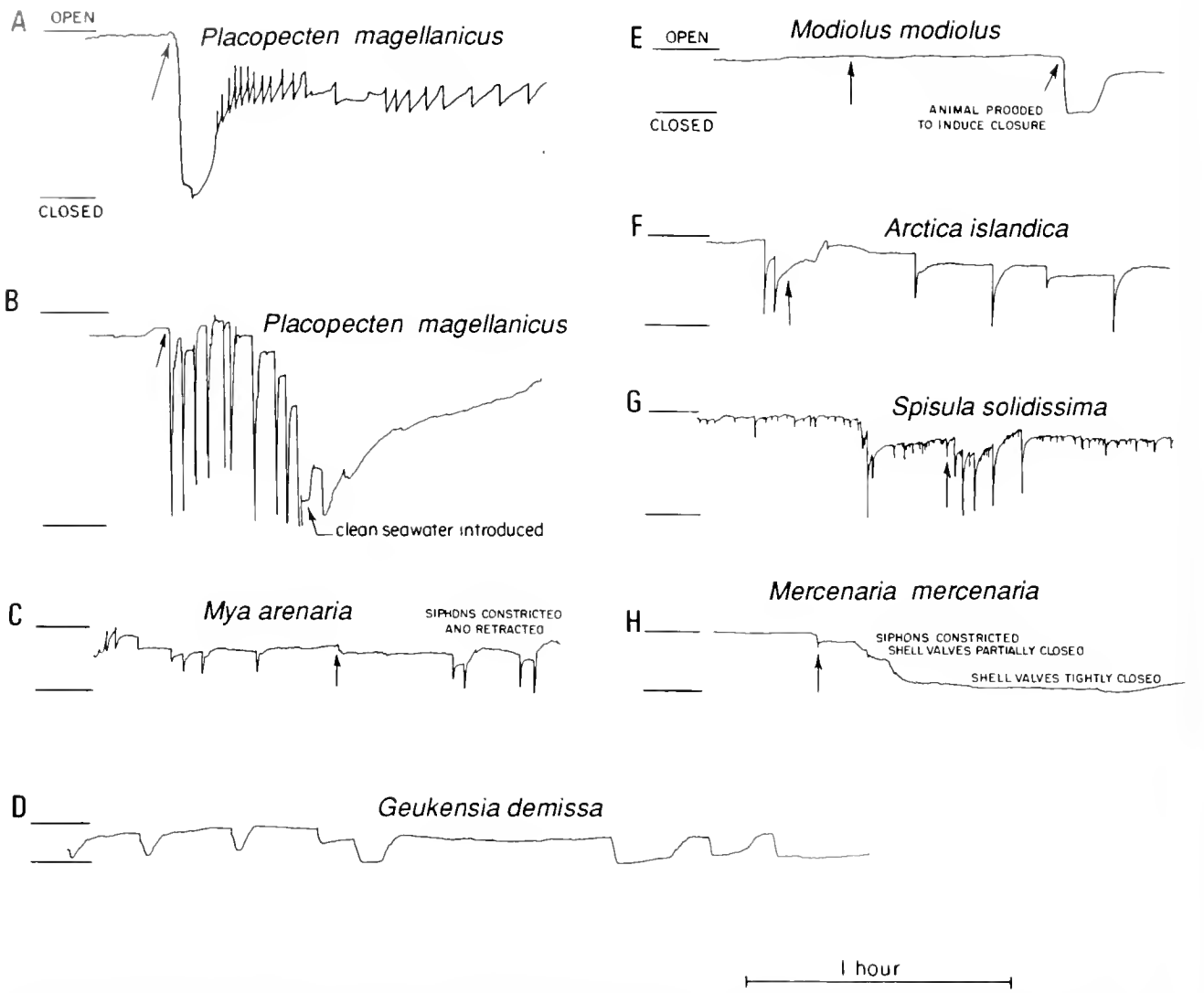

Figure 1. Tracings of shell-valve activity patterns of bivalve molluscs after exposure to *P. tamarensis*. Arrows indicate addition of GT429. After Shumway and Cucci (1987).

Effects on Filtration Rate

Reduced filtration rates have been reported for a number of bivalves exposed to a variety of toxic dinoflagellates. In general, those animals that showed increased valve or siphon closure also showed decreased filtration rates, e.g., *Mytilus edulis* from Rhode Island, *Mya arenaria* (Shumway and Cucci 1987), *Crassostrea virginica* (Ray and Aldrich 1967, Shumway and Cucci 1987), *Crassostrea gigas* (Dupuy and Sparkes 1968), and *Mercenaria mercenaria* (Dupuy and Sparkes 1968, Shumway and Cucci 1987). Filtration rates increased significantly in *Ostrea edulis* and *Mytilus edulis* from Maine, while filtration rates were unchanged in *Placopecten magellanicus*, and *Spisula solidissima* upon exposure to GT429 (Table 1, Shumway and Cucci 1987).

Effects on Feeding

In a series of feeding experiments, Shumway and Cucci (1987) found that *Mytilus edulis*, *Crassostrea virginica*, *Ostrea edulis*, *Placopecten magellanicus*, and *Modiolus modiolus* showed no preferential selection either for or against GT429, and the dinoflagellate appeared in both the pseudofeces and feces. GT429 appeared in the pseudofeces of *Mya arenaria* but was excluded from the feces, demonstrating preingestive selection (Figure 4). Exposure of *Spisula solidissima* to GT429 resulted in an increase in pseudofeces production, with GT429 appearing in both the pseudofeces and feces (Figure 5).

Byssus Production

The effects of *Protogonyaulax tamarensis* on byssus production by three species of mussles (*Mytilus edulis*, *Geukensia demissa*, *Modiolus modiolus*) were reported by Shumway et al. (1987, Table 2). Byssus production was inhibited in both *M. edulis* and *G. demissa;* moreover, there were geographic differences in the response of *M. edulis*, i.e., animals from areas previously exposed to toxic algal blooms (Maine) showed less decrease in byssus pro-

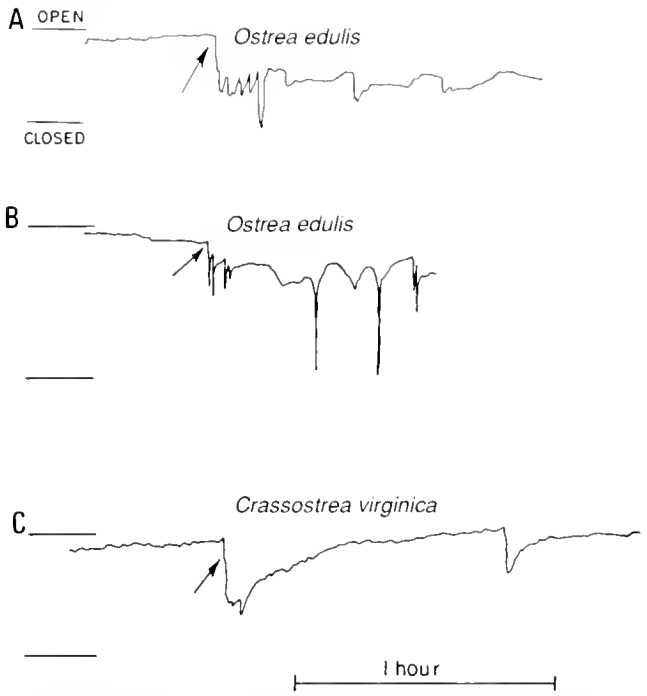

Figure 2. Tracings of shell valve activity of oysters after exposure to *P. tamarensis*. (Arrows indicate addition of GT429.) After Shumway and Cucci (1987).

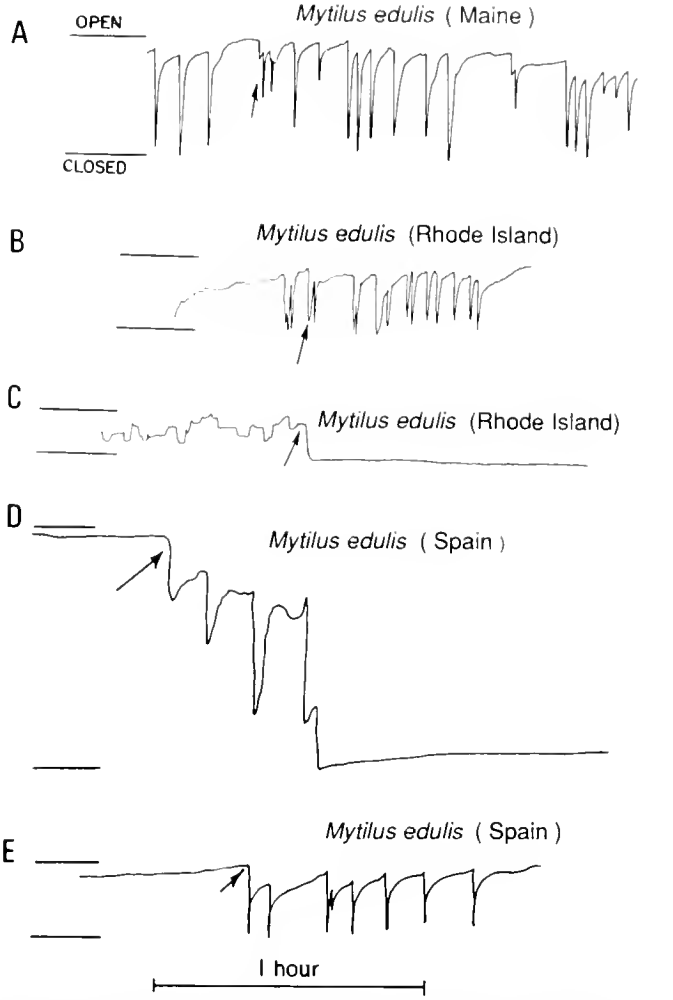

Figure 3. Tracings of shell-valve activity of mussels from various localities after exposure to *P. tamarensis*. Arrows indicate introduction of GT429. After Shumway and Cucci (1987).

duction than did mussels from areas never exposed to such blooms (Rhode Island). Only *M. modiolus* was unaffected. Shumway et al. (1987) suggested that, while the presence of toxic dinoflagellates has a definite effect on byssus production, the reduced production is not necessarily a response to the presence of toxins *per se*, or to the interruption of the byssus function in particular, but is more likely an indication of physiological stress by individual animals.

Oxygen Consumption

Oxygen consumption, after exposure to GT429, has been measured in 4 species of bivalves by Shumway et al. (1985), and the relationship between oxygen consumption and other physiological responses to red tide is not clear. For example, *Placopecten magellanicus* showed no change in filtration rate, an increase in valve activity, yet showed a decrease in oxygen consumption. *Spisula solidissima* showed no change in filtration or valve activity, yet showed a decrease in oxygen consumption. *Mya arenaria* showed a decrease in filtration rate yet an increase in oxygen consumption. *Mytilus edulis* from Rhode Island showed an increase in valve closure and an increase in oxygen consumption. Not surprisingly, *Mytilus* from Maine, which had prior exposure to *Protogonyaulax tamarensis* showed no change in oxygen consumption yet had increased clearance rates. The effects of red tide on oxygen consumption may be due to indirect effects, such as increased activity or repayment of an oxygen dept, although a direct effect on cellular metabolism cannot be ruled out in species such as *Placopecten* or *Spisula* which either showed an increase, or no change, in activity yet had a decrease in oxygen consumption (Figure 6).

Cardiac Activity

Gainey and Shumway (1988) measured cardiac activity in 8 species of bivalves exposed to GT429. Cardiac activity was unaffected in *Spisula solidissima, Mercenaria mercenaria, Placopecten magellanicas* and *Artica islandica*. In *Mya arenaria*, there was a transient decrease in heart rate between 30 min. and 3 hr. after exposure to GT429 in 4 of 10 individuals. The rates returned to normal within 24 hr., and were presumably related to increased siphon closure, which resulted in depressed heart rates in untreated individuals.

Exposure of *Ostrea edulis* to GT429 affected 2 out of 9 animals: these 2 had a significant decrease in heart rate. These animals also experienced cardiac arhythmias.

Exposure of *Geukensia demissa* to GT429 resulted in a significant decrease in heart rate in 1 out of 10 animals tested. In addition, 3 animals had a transient increase in

TABLE 1.

The clearance rates of 6 species of bivalve molluscs estimated assuming 100% retention efficiency of algal cells. Animals were fed a mixture of algal cells (*Prorocentrum minimum*, *Phaeodactylum tricornutum* and *Chroomonas salina*) initially. The same animals were later fed on the same mixture with the toxic dinoflagellate, *Protogonyaulax tamarensis* (GT429) added. See Shumway et al. (1985) for details.

Species	Clearance rate (cells l^{-1} h^{-1} × 10^3) Before exposure to GT429	After exposure to GT429
Ostrea edulis	4220*	6160
Placopecten magellanicus	5000	4980
Mya arenaria	6240*	4500
Mytilus edulis (Maine)	9020*	9900
Mytilus edulis (Rhode Island)	7470	7940
Spisula solidissima	5420	5310
Crassostrea virginica	8320*	7720

* Rate is significantly different from animals exposed to GT429 ($P \leq 0.05$)

heart rate, which appeared within 1 day after exposure, and disappeared within 2 days after exposure. After this transient increase, the heart rate returned to normal in 1 animal and was lower in the other 2.

The response of *Mytilus edulis* to GT429 was divided into one of 3 categories: maximal, transient and minimal. Of the 17 *Mytilus* from Maine exposed to GT429, 6 had a maximal response. Two of these animals had a significant decrease in heart rate, while 2 animals had a significant increase in heart rate. Two animals had a transient increase in rate, followed by a prolonged decrease. Four of the 6 animals died within 6 days of exposure. In addition to the change in heart rate, cardiac arhythmias were present in 5 of the 6 animals. Five of the 17 *Mytilus* had a transient response to GT429. The pre- and post-treatment heart rates were not different, but these animals had cardiac arhythmias, and depressed rates, but actively returned to normal within 3 days of exposure to GT429. Six of the *Mytilus* were unaffected by exposure of GT429.

Eleven *Mytilus* from Long Island were exposed to GT429. Three animals had a maximal response: 2 had a significant decrease in heart rate, and 1 had a significant increase. The 2 animals that had depressed heart rates also had pronounced arhythmias within 2 days of exposure. These arhythmias lasted for 8 days. Two of the animals had a transient response consisting of periods of cardiac arhythmia that appeared within 4 days after exposure and lasted until 5 days after exposure. Six animals had no response to GT429.

The 3 species that had an unequivocal response to GT429 are pteriomorphs (Table 3). The only heterodont that had a response to GT429 was *Mya arenaria:* 40% of the individuals tested had a reduced heart rate for several hours after exposure. In *Mya,* siphon closure is accompanied by bradycardia prior to exposure to GT429, and this transient reduction in heart rate probably was due to closing of the siphons in response to GT429. The different response of pteriomorphs and heterodonts to the presence of GT429 is reflected in other aspects of their cardiac physiology (reviewed in Painter and Greenberg 1979).

Neurophysiological Effects

The effect of red tide toxins on bivalve neurons has been investigated by Twarog and Yamaguchi (1974, Table 4). They found a graded response that varied according to species. *Mytilus edulis, Placopecten magellanicus,* and *Mercenaria mercenaria* were unaffected by concentrations of saxitoxin (STX) less than or equal to 0.1 mM. *Mya arenaria* neurons were inhibited by 0.01 mM, while *Crassostrea virginica* neurons were inhibited by 0.1 uM STX. Twarog and Yamaguchi hypothesized that those animals that are most sensitive to STX either are not regularly exposed to the toxin, or have a reduced filtration rate which would reduce accumulation of toxin. This hypothesis is borne out by the fact that *Mytilus edulis* rapidly accumulates toxin and is insensitive to STX, whereas the rate of accumulation in *Mya* is less (Shumway and Cucci 1987).

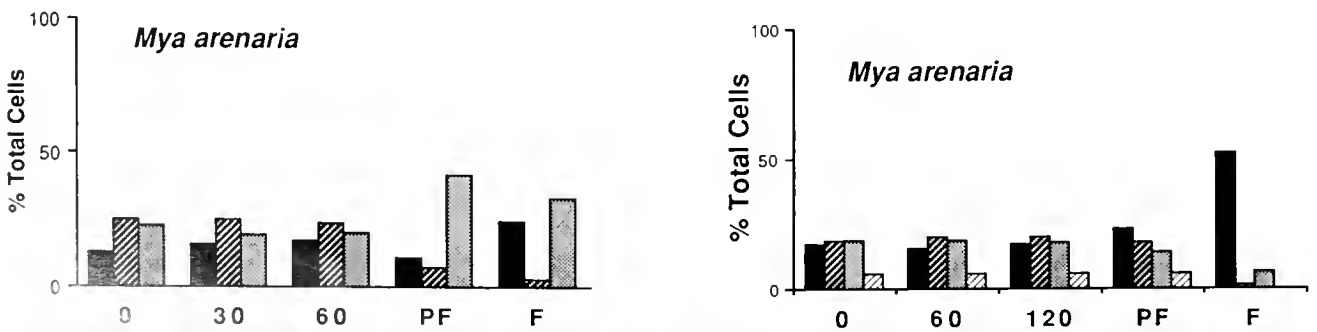

Figure 4. Percentages of the total cell count within an algal mixture of the clones 3H (solid bars), 3C (dark stripes), Exuv (hatched) and GT429 (light stripes) at time 0 and after 60 and 120 min. and within the pseudofeces (PF) and feces (F) during feeding experiments. After Shumway and Cucci (1987).

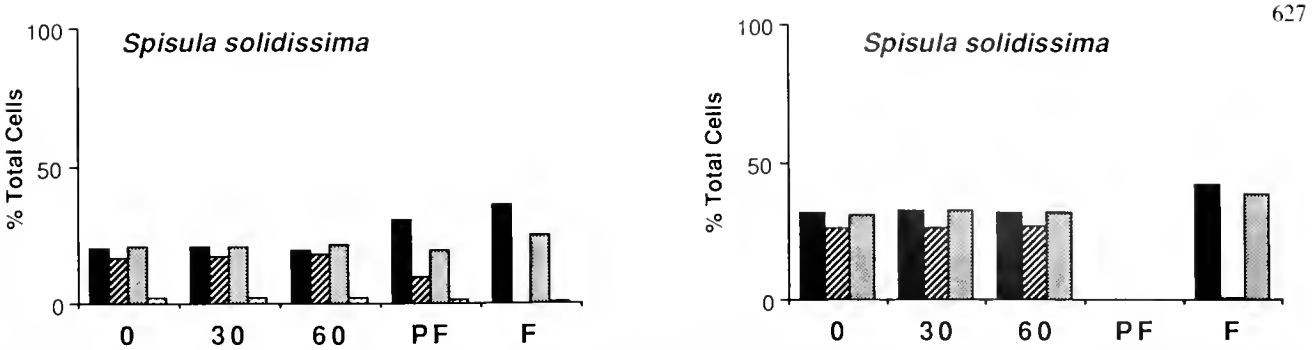

Figure 5. Percentages of the total cell count within an algal mixture of the clones 3H (solid bars), 3C (dark stripes), Exuv (hatched) and GT429 (light stripes) at time 0 and after 60 and 120 min. and within the pseudofeces (PF) and feces (F) during feeding experiments. After Shumway and Cucci (1987).

TABLE 2.

The production of byssus threads by three species of mussels before (control) and after exposure to *Protagonyaulax tamarensis* and after a 1 week recovery period. Results are expressed as number of threads produced per mussel per day ± standard deviation (from Shumway et al. 1987).

Species	n	Control	After exposure to GT 429	After recovery
Mytilus edulis (Maine)	94	15.5 ± 2.1	7.1 ± 3.4*	13.4 ± 4.5
Mytilus edulis (RI)	91	6.2 ± 1.2	1.9 ± 0.8†	2.4 ± 1.0†
Modiolus modiolus	92	21.9 ± 4.9	23.2 ± 3.5	23.6 ± 4.8
Geukensia demissa	86	19.4 ± 4.1	10.6 ± 1.1*	16.3 ± 3.3

* Significantly different from control at $p < 0.05$.
† Significantly different from control at $p < 0.01$.

TABLE 3.

Summary of effects of the toxic dinoflagellate, *Protogonyaulax tamarensis*, on cardiac activity in bivalve molluscs. Inh: Inhibition; Exc: Excitation; Tran: Transient; None: No effect (From Gainey and Shumway, 1988).

Subclass	Species (n)	Response: %
Pteriomorpha	*Mytilus edulis* (Maine n = 17)	Tran. Inh: 29%
		Inh: 24%
		Exc: 12%
		None: 35%
	Mytilus edulis (Long Island n = 11)	Tran. Inh: 18%
		Inh: 18%
		Exc. 9%
		None: 55%
	Geukenia demissa (n = 10)	Tran. Inh: 10%
		Inh: 10%
		Tran. Exc. 40%
		None: 40%
	Ostrea edulis (n = 9)	Inh: 22%
		None: 73%
	Placopecten magellanicus (n = 6)	None: 100%
Heterodonta	*Mya arenaria* (n = 10)	Tran. Inh: 40%
		None: 60%
	Spisula solidissima (n = 4)	None: 100%
	Mercenaria mercenaria (n = 16)	None: 100%
	Arctica islandica (n = 6)	None: 100%

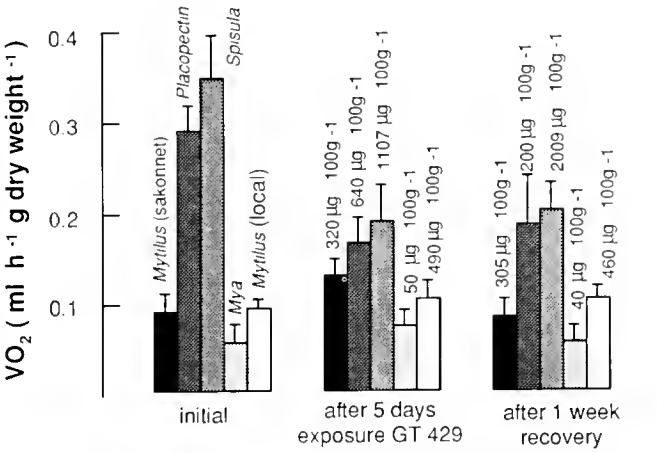

Figure 6. Rates of oxygen consumption for 4 species of bivalve molluscs exposed to the toxic dinoflagellate, *P. tamarensis*. After Shumway et al. (1985).

TABLE 4.

Block of action potential by saxitoxin (STX) (From Twarog and Yamaguchi, 1974).

Species	10^{-8}	10^{-7}	10^{-6}	10^{-5}	10^{-4}
Mytilus edulis	–	–	–	–	–
Placopecten magellanicus	–	–	–	–	–
Mercenaria mercenaria	–	–	–	–	–
Modiolus demissus	–	–	–	–	+
Pecten irradians	–	–	–	–	+
Mya arenaria	–	–	–	+	+
Crassostrea virginica	–	+	+	+	+
Elliptio complanata	–	+	+	+	+

The species are listed in order of increasing sensitivity to STX.
+ = Full Block.

There have been periodic reports in the literature of mass mortality of a variety of bivalves exposed to a variety of toxic dinoflagellates. However, the effects of the various red tide organisms are variable. For example, Sievers (1969) reported that *Carassostrea virginica* showed increased mortality when exposed to *Gonyaulax poleydra;* similarly, Reish (1963) reported increased mortality of *Mytilus edulis* exposed to *Gonyalulax poleydra,* while Adams et al. (1968) reported no deaths for *Mytilus* exposed to *Protogonyaulax tamarensis.* In a laboratory study, there was 75% mortality in *Mytilus edulis* from Rhode Island and Spain upon exposure to *P. tamarensis.* These mussels had had no prior to exposure *P. tamarensis.* In contrast, there was no mortality in *Mytilus edulis* from Maine upon exposure to *P. tamarensis.* These mussels had had prior exposure to the toxic dinoflagellate (Shumway and Cucci 1987).

SUMMARY

The most common effect of red tide upon bivalves is a decrease in exposure to the environment either by reducing filtration, or increasing valve closure. The other physiological effects noted, such as changes in oxygen consumption and cardiac activity, may be associated with the former responses and may not be a direct effect of exposure to red tide organisms. However, whether or not toxic dinoflagellates exert their physiological effects directly, or indirectly, they clearly cause physiological stress in a variety of bivalve molluscs.

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A CASE FOR SEQUESTERING OF PARALYTIC SHELLFISH TOXINS AS A CHEMICAL DEFENSE

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ABSTRACT Captive starlings were fed butter clams (*Saxidomus giganteus*) of high, low, and no toxicity to investigate the response of predators to prey containing paralytic shellfish toxins sequestered from *Protogonyaulax* spp. Birds fed siphons from highly toxic *S. giganteus* (>900 μg STX/100 g) either refused to consume >0.6–0.9 g of tissue during a 24 hr. period and survived, or died within 24 hr. following the ingestion of 0.6–4.0 g. Control starlings consumed all available siphons from low toxicity and non-toxic *S. giganteus* during the same period and showed no ill effects. Our results suggest that PSP toxins could function as an effective predator defense in prey capable of sequestering the neurotoxins and may limit the distribution and abundance of species that either avoid or die from eating these prey. In light of the importance of sodium channels and their sensitivity to saxitoxin in most metazoans, such predators could include a wide range of both vertebrates and invertebrates.

KEY WORDS: paralytic shellfish poisoning, chemical defense, predation, birds, mortality, butter clam, *Saxidomus giganteus*, starlings, *Sturnus vulgaris*

INTRODUCTION

Paralytic shellfish toxins (PST) produced by toxigenic dinoflagellates have been shown to move through marine food chains and accumulate in a variety of marine organisms; e.g., bivalves, crab, fish, gastropods, starfish, polychaetes, zooplankton (Halstead 1978, Davies 1986, Jonas-Davies and Liston 1985, Erickson 1988, White 1977, White 1980). Although the risk to humans from eating bivalves contaminated with PST has been well documented worldwide (Quayle 1969, Baden 1983, WHO 1984), the biological significance of the sequestering of these toxins is poorly understood.

Fish kills associated with "red tide" blooms are the best documented predator–prey relationship known to be influenced by dinoflagellate toxins (White 1977, 1980, 1981) and the link between dinoflagellates, grazing zooplankters and planktivorous fish mortality has been experimentally demonstrated (Yazdandoust 1985, Erickson 1988). Other, anecdotal accounts of predator mass mortalities involving birds (McKernan and Scheffer 1942, Coulson et al. 1968, Bicknell and Collins 1972, Bicknell and Walsh 1975, Armstrong et al. 1978, Hockey and Cooper 1980, Nisbet 1983), fur seals and foxes (Keyes 1965), sea otters (DeGange and Vacca in preparation) and whales (Beach 1988) also implicate dinoflagellate toxins. This broad array of important, upper trophic level taxa suggest profound and far reaching ecological consequences of blooms of toxic dinoflagellates, particularly those in the genus *Protogonyaulax*.

Although the anecdotal accounts do not document the presence of PST in the bodies of victims (excepting Beach 1988), they are supported by our understanding of the action of *Protogonyaulax* toxins at the cellular level. Extremely low concentrations of saxitoxin (STX) and its derivatives have been shown to block sodium channels, which are critical to neuronal activity in invertebrates and activation of both skeletal muscle and nerve cells in vertebrates (Hille 1984). Because of their generally uniform structure, function and STX-sensitivity in all metazoans (Hille 1984), we may expect a strong predator response, especially among vertebrates, to prey containing STX-based toxins. Although toxicological studies involving injection or forced ingestion of PST extracts into various vertebrates resulted in mortality from respiratory paralysis (see Halstead 1978), controlled feeding experiments are required to determine the actual physical and behavior responses of whole organisms to toxic prey. Other than the works of Erickson (1988) and Yazdandoust (1985) in which fish died when fed toxic zooplankton, there are no other feeding studies involving higher trophic level species in dinoflagellate based food chains.

In this study, starlings (*Sturnus vulgaris*) were fed siphons from butter clams (*Saxidomus giganteus*) containing known amounts of STX. Although starlings are not important marine predators, the generic nature of sodium channels and their sensitivity to STX suggest that the responses from starlings may be generalizable to other birds (e.g., scoters, oyster catchers and gulls) known to be significant consumers of bivalves (Davidson 1968, O'Connor and Brown 1977, Vermeer 1982, Nettleship et al. 1984) and other marine prey that do become toxic. The results also may be relevant to other vertebrate predators such as fish (Peterson and Quammen 1982) and sea otters (Kvitek

and Oliver 1988) which prey on these same species. Furthermore, only by analyzing tissues of known paralytic shellfish poisoning (PSP) victims for toxin content can we determine the reliability of these methods in linking naturally occurring mortalities to PST.

METHODS

Thirteen adult starlings were captured in Seattle, Washington during May (n = 6) and again in June (n = 7) 1988. The birds were kept in individual cages (40 × 26 × 22 cm) in aviaries on the roof of Kincaid Hall at the University of Washington, and fed ad libitum a pre-experimental diet of dried cat chow (Friskies Ocean Fish Flavor Delicious Cat Dinners) and water for 5–10 days.

Highly toxic butter clams were collected from the intertidal at middleground bar, Sequim Bay, Washington on May 16 and June 18, 1988. Butter clams from this site have been found to contain consistently high levels of PST year round for the last 4 years (1987–88 mean ± SD and range 615 ± 455 μg STX/100 g and 200–1400 respectively, Washington State Department of Health unpublished data). Low toxicity butter clams were collected at Port Gamble, Washington on May 17, and non-toxic clams at Mukilteo, Washington on June 19, 1988. All clams were kept in filtered, recirculating sea water.

The first experiment involved six birds, 3 experimental and 3 controls chosen at random. Siphons were removed from 12 highly toxic clams, blotted dry, cut lengthwise into narrow strips, and thoroughly mixed. The strips were then subdivided into 6 portions (~7 g each) and weighed to the nearest 0.01 g on a Sartorius digital analytical scale. Three portions were for the 3 experimental birds, 2 portions were to set out in identical containers but unavailable to the birds to determine weight change due to water loss; and 1 portion was frozen at −10°C and saved for toxin content analysis. The siphons of low toxicity were similarly prepared and divided into 5 portions, three for the control birds, one for toxin analysis, and one water loss control.

The first feeding was at 0700 hr. May 20. Water, but no other food was made available. A second portion, prepared as before but with only one water loss control, was given after 6 hr.

The condition of the birds was checked following 24 hr., and all remaining food was collected and weighed for each bird. Weights were corrected to wet meat weight based on the mean weight loss of the water loss control samples. All surviving birds were given ad libitum water and cat chow, and observed for an additional 5 days. The kidneys, liver, heart, and digestive tract (esophagus to anus) were removed from the one experimental victim within 30 min. of its death. The same tissues were removed from one starling not fed toxic food. All tissues were analytically weighed and frozen at −10°C until toxin analysis.

This experiment was repeated again with the following modifications. On June 20, seven starlings were given ad libitum water and non-toxic siphons prepared as above with 3 water loss controls and one portion for toxin analysis. Following 24 hr., the remaining food was collected and weighed, and the conditions of the birds were observed. At this time, 4 experimental birds were selected at random and given highly toxic siphons and the other three birds non-toxic siphons. The birds were then observed periodically over the next 24 hr. At the end of this period, the remaining food was collected and weighed and the surviving birds, both controls, were given highly toxic siphons and observed. The remainder of this food was collected and weighed after another 24-hr. period. The weight of dead birds was measured to the nearest 0.01 g.

Bird organs, except the digestive tracts, and samples of siphon diets were analytically weighed, homogenized in 0.20 N HOAc (1:2, w/v), and centrifuged at 2100 × g for 10 min. in a Beckman Model TJ-6 centrifuge. Intestinal contents from thawed digestive tracts were separately squeezed out into tared vials. Each digestive tract was cut open, the luminal surface was gently rubbed under cold, running tap water to thoroughly remove any residual material, and damp dried. The intestinal walls and their contents were separately weighed and homogenized as above. Supernatants were filtered with MPS-1 Micropartition Systems equipped with YMT membranes (25–30,000 MW cut off). Permeates were stored at −41°C until high pressure liquid chromotography (HPLC) analysis.

Samples were analyzed for saxitoxin (STX) three times on different days by the HPLC method of Sullivan and Wekell (1987). A STX secondary standard (diluted from STX obtained from the Food and Drug Administration: Cincinnati, OH) was employed after being quantified with a mixed PST standard coded MS-33; 1:20 (FDA, Seattle, WA). STX concentrations were expressed as mean ± SD of nmol STX/g tissue and converted to μg STX equivalents/100 g tissue, total μg STX, or μg STX/kg body weight by the method of Sullivan et al. (1985). Only STX was quantified because it is the major toxin in the siphon of butter clams (Schantz et al. 1957, 1966). The weight of food consumed by the birds was determined by correcting for water loss and used to calculate the quantity of STX ingested.

RESULTS

In the first experiment, 6 hours after the initial feeding, the control starlings had consumed almost all their food, whereas the experimental birds had scattered some of their food but little appeared to have been eaten.

After 24 hr., the control and treatment diets had decreased in weight by 72 ± 2% (mean ± SD) due to water loss. The control birds had eaten all food (13.6 ± 0.6 g/bird; mean ± SD) except for a few unavailable pieces (0.2–2.0 g) which had fallen out of their cages or were under the paper cage lining (Table 1). Two of the experimental birds had eaten <1 g each and the third had con-

TABLE 1.

Feeding Experiment 1. During a 24-hr. period, experimental starlings either shunned high toxic butter clam siphon tissue after eating much less than controls fed low toxic siphons, or died. The amount of saxitoxin (STX) consumed by each bird was calculated from the concentrations found in the food.

Treatment	Food given g	Food eaten g	STX consumed µg	Response
Experimental				
Bird 1	16.5	0.6	5.5	None
Bird 2	16.3	0.9	8.3	None
Bird 3	16.5	4.0	37.0	Death
Control				
Bird 4	14.9	12.9	11.5	None
Bird 5	14.0	13.8	12.3	None
Bird 6	15.2	14.1	12.5	None

sumed only 4.0 g (Table 1). The latter bird sat quietly, with ruffled feathers and did not startle when people came into view as did all the other birds. It had lost motor coordination and during the last hr. went into sporadic spasms, characterized by uncontrolled flapping and then died.

The highly toxic and low toxicity siphons used in the first study were 925 ± 38 and 89 ± 2 µg STX/100 g tissue respectively (means ± SD). Birds which showed no ill effects had ingested <12.6 µg STX (Table 1). The bird that died consumed 691 µg STX/kg body weight. Toxin was detectable in very low amounts in the intestinal contents (21.8 ± 3.0 µg STX) and digestive tract wall (0.62 ± 0.12 µg STX) of the experimental victim. Less than 2 µg STX/100 g (the lower limit of detection) was found in the kidney, liver, and heart of the bird fed highly toxic siphons and in the organs and gut contents from the control bird.

In the second feeding study, the toxic and non-toxic siphons contained 1260 ± 80 and <2 µg STX/100 g tissue respectively. During the first 24 hr period, all birds readily ate non-toxin siphons (Table 2). During the second 24 hr., all 4 treatment birds died following consumption of <2 g of highly toxic siphons. One of these consumed <0.6 µg STX, showed no symptoms of STX poisoning and died within 3 hr. of the feeding. The 3 controls consumed all available siphons and one died. The control victim also showed none of the symptoms observed in the first experiment. During the third 24 hr. period when the remaining controls were fed highly toxic siphons, both showed PSP symptoms and died after consuming <3 g. Birds which displayed PSP symptoms ingested 7.2–32.4 µg STX (148–606 µg STX/kg body weight). Except for bird 6, STX was detected in the intestinal walls or contents of all experimental victims which exhibited PSP symptoms.

DISCUSSION

Although starlings do not prey on bivalves, the experimental birds readily ate the low toxicity and non-toxic butter clam siphons. Our results suggest that the experimental birds detected PST in the highly toxic siphons and as a result, consumed significantly less food than the control subjects. If the experimental birds had an innate or learned aversion to the PST, hunger and a lack of alternative food may have forced the subjects to eat the contaminated siphons. Additional research is needed to determine whether starlings could distinguish between non-toxic and toxic siphons and select the former.

The starlings varied in their responses to the highly toxic siphons. In the first study, 4 birds consumed 8.3–12.5 µg STX and survived, but one starling in the second study showed PSP symptoms and died after eating only 7.2 µg STX in 14–24 hr. This variation may be due to differences in the weights, ages, and sexes of the birds. McFarren et al. (1956) noted rats varied in survival with strain and weight following oral administration of PST. The greater sensitivity of the birds to STX in the second experiment may also have been related to the physiological stress associated with the completion of their breeding season and compounded by confinement in small cages. This is suggested by the absence of PSP symptoms in the deaths of birds #1 and 5 (an experimental and a control) during the second study.

Although the average amount of PST which killed the starlings was higher on a per body weight basis (Table 2) than for most mammals and 3× greater than for pigeons (McFarren et al. 1956), the amount that killed our subjects should not be interpreted as the lethal dose for starlings. The birds in this study were fed ad libitum and thus their PST detection/rejection threshold (the point at which they refuse to eat any more toxic food) may have been higher than the lethal dose. In fact, the intestinal walls or contents of the victims, except bird 6, still contained STX (Table 2) which suggests a lethal dose lower than the toxin consumed.

HPLC analysis of the intestinal contents may be a useful method for implicating PSP as the cause of death in naturally occurring mortalities. Most of the intestinal contents of the starlings which displayed PSP symptoms contained STX, but the hearts, kidneys and livers lacked detectable concentrations of STX. The kidneys and livers were analyzed because it was suspected that these tissues might filter, sequester or metabolize PST as detoxification mechanisms. Prinzmetal et al. (1932) noted 40% of the PST orally administered to a dog was excreted in its urine in only 2 hr.

Analyzing the intestinal wall for PST in a possible PSP victim may produce mixed results. Toxin identified in the intestinal walls may have resulted from STX migrating from the lumens into the tissue during freezing and thawing of the intact digestive tracts before the contents were removed. This migration was noted in adductor muscles of PST infested scallops (Patinopecten yessoensis) (Noguchi et al. 1984). If the intestinal contents of a suspected PSP

TABLE 2.

Feeding Experiment II. During the 1st 24 hr. all birds consumed all available non-toxic siphons with no ill effects. During the 2nd 24 hr., experimental birds given highly toxic siphons consumed much less than controls and died. Previous controls given highly toxic siphons during the 3rd 24 hr. also died. STX (n = 3 runs/sample) only could be detected in the intestinal tract wall and intestinal tract contents of the victims exhibiting PSP symptoms (sitting quietly with ruffled feathers, absence of startle response, loss of motor coordination, spasms). These symptoms were not observed in the one experimental bird that died after eating <0.1 g or in the single control victim.

Time period Treatment Subject	Food given g	Food eaten g	STX consumed		STX contents		Hr. until death	PSP symptoms	Body weight at death g
			Total µg	Per body wt µg/kg	Intestinal wall µg STX	Intestinal contents (mean ± SD)			
1st 24 hr.									
Experimental (non-toxic siphons)									
Bird 1	8.0	8.0	a					None	
Bird 2	7.9	7.9	a					None	
Bird 3	8.0	6.8	a					None	
Bird 4	8.0	8.0	a					None	
Control (non-toxic siphons)									
Bird 5	8.2	8.2	a					None	
Bird 6	8.1	8.1	a					None	
Bird 7	8.1	8.0	a					None	
2nd 24 hr.									
Experimental (highly toxic siphons)									
Bird 1	11.8	<0.1	<0.6	<9	b	b	3	None	64.8
Bird 2	12.1	1.4	18.0	306	1.60 ± 0.16	1.70 ± 0.10	6	Present	58.9
Bird 3	11.5	1.5	19.4	336	b	0.12 + 0.00	12–24	Present	57.8
Bird 4	11.7	1.4	17.8	332	1.00 ± 0.20	0.79 ± 0.10	24	Present	53.7
Control (non-toxic siphons)									
Bird 5	12.2	12.0	a		b	b	12–24	None	51.9
Bird 6	12.2	11.9	a					None	
Bird 7	12.2	11.7	a					None	
3rd 24 hr.									
Previous controls (highly toxic siphons)									
Bird 6	7.4	0.6	7.2	148	b	b	14–24	Present	48.6
Bird 7	7.4	2.6	32.4	606	0.47 ± 0.06	0.28 ± 0.01	12	Present	53.5

a = <0.2 µg STX
b = <2 µg STX/100 g tissue

victim contained trace or nondectable amounts of STX, the intestinal wall may not contain a quantifiable concentration of the toxin. This is supported by the finding that the intestinal contents of bird 3 possessed a very low amount of STX but the intestinal wall lacked a detectable concentration of STX. Of course, if the suspected PSP victim did not ingest sufficient toxin or the PST are absorbed and/or degraded during digestion, the HPLC analysis of the intestinal contents will not help link PST to the cause of death. This was exemplified by bird 6 which ate a small amount of STX, showed PSP symptoms but lacked a detectable concentration of PST in the intestinal contents after 24 hr.

Ecological Implications

These results suggest that the movement of dinoflagellate produced neurotoxins through the marine food web may have profound implications for some predator–prey interactions. Mechanisms could involve either predator mortality or prey avoidance. PST have been shown to accumulate in bivalves and other important marine prey species (Quayle 1969, Halstead 1978, Jonas-Davies and Liston 1985, Davies 1986). Because STX and its derivatives block sodium channels, PSP may be a risk common to vertebrate predators foraging on prey which accumulate these toxins. Even if the occurrence of PST is seasonal in most shellfish, occurring only during and shortly after a toxic dinoflagellate bloom (Quayle 1969, Halstead 1978, Sullivan 1982, Shumway et al. 1988), it could still influence predator mortality, distribution, abundance and feeding habits during those periods. Furthermore, episodic mass mortality from PSP could be extremely important to the population biology of long lived predators as suggested by Hockey and Cooper (1980) for oyster catchers. Seasonal avoidance of prey during critical life history stages could also be significant to some prey populations.

These ecological consequences may be greatly magnified by species that retain dinoflagellate toxins for long periods. Examples of prey sequestering toxins from their food which in turn deter predators are well documented in the plant-insect literature (Harborne 1982) and in some other marine systems (see Van Alstyne and Paul in press). The

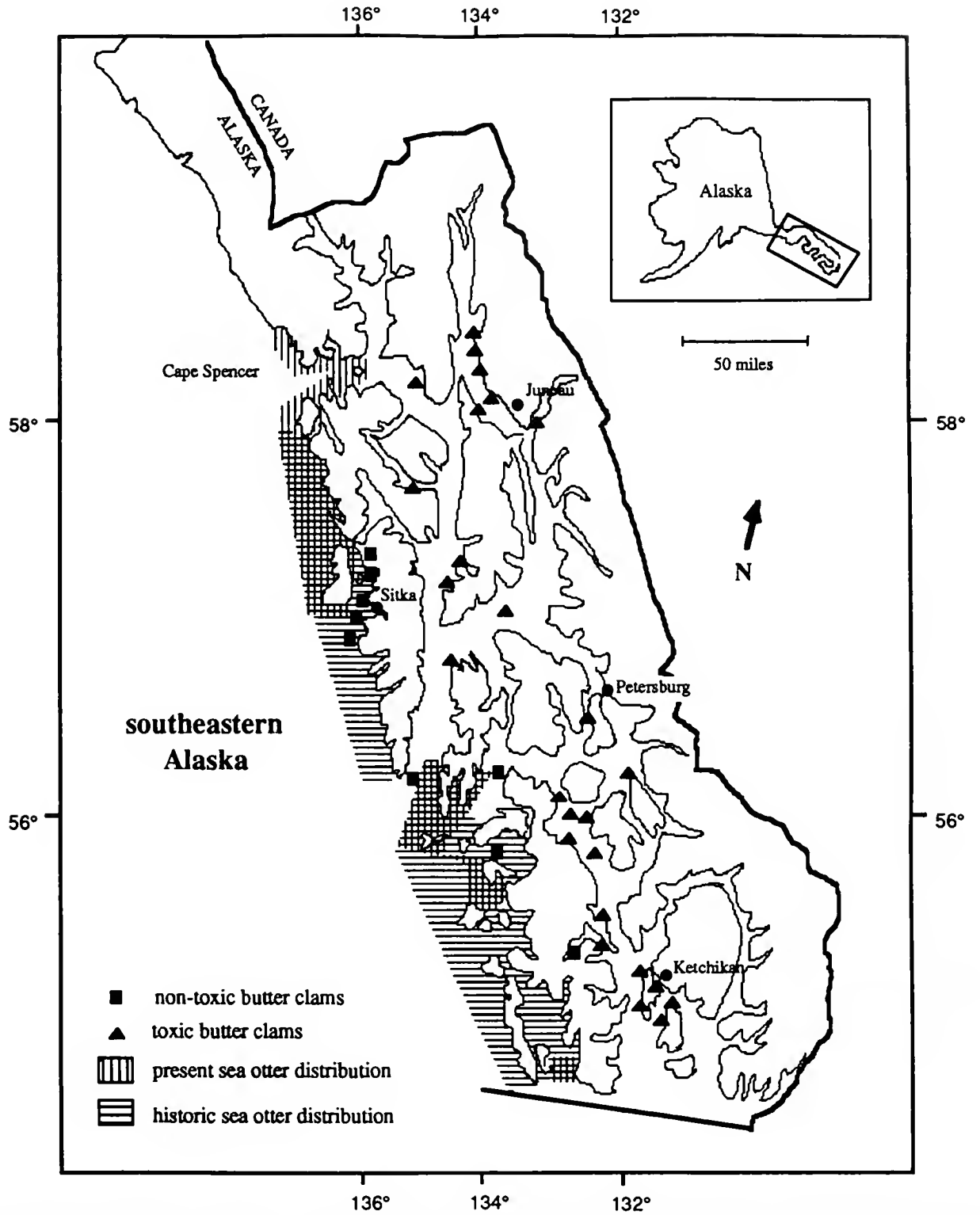

Figure 1. Map of southeastern Alaska showing the present (Pitcher 1987) and historic (Kenyon 1969, Maynard 1898, Petroff 1898) ranges of sea otters, and the geographic distribution of toxin-free and PST infested butter clams (>80 μg STX/100 g) (Chambers and Magnusson 1950, Alaska Dept. of Environmental Conservation, Div. Environmental Health, Palmer, Alaska, unpublished data). Sea otters have only been observed along the outer coast, where butter clams are not toxic, and have never been observed in the inside waters of southeast Alaska, where butter clams are also abundant but contain PST year round.

butter clam (*Saxidomus giganteus*) may be a species in which retention of PST has evolved as a chemical defense. Not only can *S. giganteus* sequester PST for >1 yr. once exposed to a bloom (Chambers and Magnusson 1950, Chambers et al. 1955, Quayle 1969) but there is also evidence that it transforms the less toxic gonyautoxins produced by *Protogonyaulax* spp. into STX (Beitler 1988, and see Shimizu et al. 1978), a much more lethal toxin (Boyer et al. 1986). STX accounts for the majority of the toxin in contaminated butter clams, and, unlike most other bivalves that become toxic, is sequestered in the siphon (Quayle 1969, Beitler 1988). Butter clams also differ from most other species of bivalves that have been investigated in its ability to feed vigorously on toxigenic dinoflagellates without showing any apparent negative response (Beitler 1988, Shumway and Gainey in press). Furthermore, the nerves of a close relative, *Saxidomus nuttalli*, have been shown to be highly resistant to TTX (the puffer fish toxin, tetrodotoxin, which binds to the same sodium channel site as STX) (Twarog et al. 1972).

The retention of STX in the siphon suggests a mechanism by which a secondarily acquired PST defense could evolve. Because siphon cropping has been shown to contribute significantly to the diets of fish and to be an important source of partial predation for clams (de-Vlas 1985, Barton 1986, Hines and Comtois 1983, Peterson and Quammen 1982), toxins placed in the siphon could reduce tissue loss to STX-sensitive predators. However, once evolved in response to partial predation, retention of such a lethal toxin could become highly effective against all sensitive predators.

The year-round toxicity of the butter clam in *Protogonyaulax* spp. bloom areas combined with the seasonal toxicity of other prey species may profoundly influence the distribution and abundance of some predators. This could be true of the sea otter (*Enhydra lutris*) in southeast Alaska (Figure 1). Although the butter clam is found in great abundance throughout southeast Alaska, it and other bivalves only become toxic in the inside passage due to annual dinoflagellate blooms; butter clams and other shellfish from the outer coast are rarely toxic (Chambers and Magnusson 1950, Magnusson and Carlson 1951, Alaska Department of Environmental Conservation, Division of Environmental Health unpublished data) (Figure 1). Sea otters, which feed almost exclusively on butter clams around Kodiak, Alaska (Kvitek and Oliver 1988) and extensively in southeast Alaska (Kvitek unpublished data) have never been reported to occur in the inside waters of southeast Alaska; historically (Maynard 1898, Petroff 1898, Kenyon 1969) or since their reintroduction (Pitcher 1987). This is in contrast to the Kodiak area where PSP is a very rare occurrence (Alaska Department of Environmental Conservation, Division of Environmental Health unpublished data), sea otters are found in both inside and outside waters (A. DeGange, USFWS unpublished data), and butter clams are rare in areas occupied by otters for more than a few years (Kvitek and Oliver 1988, Kvitek et al. in prep.). If sea otters are sensitive to PST, chronic high levels of toxins in a principal prey species combined with seasonal toxicity in most other species of bivalve prey may account in part for the absence of sea otters throughout the inside waters of southeast Alaska.

Before the hypothesis of PSP as a chemical defense can be accepted, additional experiments must be conducted using appropriate predators to determine their sensitivity and response to PST. It is quite possible that some predators may have developed an insensitivity to the toxins. This could be a permanent condition selected for evolutionarily, or an inducible response as a result of sub-lethal exposure as adults or during development. Rats given a sublethal oral dose of PST became less sensitive to subsequent doses (McFarren et al. 1956). Hille (1984) reviews a number of vertebrate and invertebrate species and tissues having sodium channels that exhibit some insensitivity to STX and TTX. Not surprisingly, the most insensitive species are generally those known to accumulate high levels of STX and TTX (Twarog et al. 1972).

Although the experimental starlings shunned shellfish containing STX or died from eating them, until we know which species are sequestering paralytic shellfish toxins, and what the physiological and behavioral responses to these toxins are for the appropriate species, the potential role of PST in predator–prey relations shall remain vague. *Placopecten megallanicus* and *Spisula solidissima*, two of the 3 species that showed little or no negative response to PST in a survey of 21 bivalve molluscs (Shumway and Gainey in press), are also known to sequester PST for >1 yr. (Medcof et al. 1947, Blogoslawski and Stewart 1978, Shumway et al. in press). These species, along with the butter clam and possibly other long-term sequesterers of PST, should be investigated in future feeding experiments to test a variety of invertebrate and vertebrate predators.

In terrestrial communities plant toxins have long been recognized to provide secondary defense for plant predators, following sequestering and accumulation. Perhaps the cardiac glycosides provide the greatest array of examples (Harborne 1982). Similar examples exist in which defensive attributes acquired from a prey are used by its predator to inhibit or discourage its own consumer. Our report suggests the real possibility of a highly escalated influence where dinoflagellate toxins are involved, since death is likely. The most general ecological consequence may be exclusion from an otherwise occupiable portion of its geographic range as in the sea otter, rather than a pattern of local extinction coupled with behavioral avoidance.

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PARALYTIC SHELLFISH MANAGEMENT PROGRAM IN BRITISH COLUMBIA, CANADA

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ABSTRACT An overview of the paralytic shellfish management program in British Columbia is presented. A risk assessment model in terms of the response time and the extent of a monitoring program is proposed.

KEY WORDS: risk assessment, response time, monitoring stations, British Columbia

INTRODUCTION

Blooms of toxic dinoflagellates belonging to the genus *Protogonyaulax* (Taylor 1984) do occur in British Columbia. Accumulation of their cells by filter feeding bivalve molluscs and the subsequent consumption of these shellfish by humans can lead to outbreaks of paralytic shellfish poisoning (PSP). The federal Department of Fisheries and Oceans has compiled paralytic shellfish toxicity records in British Columbia since 1942 (Quayle and Bernard 1966, Quayle 1969). While the frequency and intensity of toxic dinoflagellate blooms varies from year to year, the probability of having a toxic bloom somewhere along the British Columbia coast approaches certainty at a given year. The challenge for any monitoring program is to detect when and where a bloom occurs.

The monitoring program in the State of Maine involves weekly sampling of mussels and soft shell clams from selected locations during April–October (Shumway et al. 1988). Similar sampling programs are also established in the Pacific Rim shellfish producing states of Washington, Oregon and California. The monitoring program in Hong Kong focusses on its ability to respond rapidly to reported sightings of red tide. On-site verification are conducted by a "mobile squad" capable of species identification and toxicity testing (Wong and Wu 1987).

PROGRAM OBJECTIVES AND COMPONENTS

The Canadian Sanitary Shellfish and Toxicity Management Program in British Columbia can be highlighted by five major functional components:

1. Shellfish toxicity monitoring,
2. Sanitary shellfish growing water classification,
3. Processor certification, including harvesting, transportation and product control,
4. Patrol and enforcement on-site,
5. Communication and response.

The objectives of the Canadian program, in the context of shellfish toxicity monitoring, are as follows:

1. Public Safety: to provide reasonable assurance that shellfish harvested from open areas are not toxic; and
2. Resource Utilization: to promote the best use of shellfish resources and optimize the long term economic return to Canada.

By providing a safe shellfish product to the consumer, a sound shellfish toxicity management program achieves not only the first objective, but also re-inforces the second objective by enhancing consumer demand. In marketing terms, a demand pull is created through the establishment of a consistant and credible product reputation. The integrity of bivalve fisheries can only be preserved through a deligently managed shellfish program that encompasses both public safety and resource management concerns.

GOAL PATHS

To achieve the stated objectives, a paralytic shellfish (PS) management program must be able to DETECT and RESPOND to toxic blooms in a timely manner. Open areas must be monitored.

Risk Assessment

The risk to public health is a function of the extent of a monitoring program and the response time required to implement closure actions:

$$\text{Risk (r)} \propto \frac{\text{Response time (t)}}{\text{Monitoring (m)}} \qquad (1)$$

where

Risk (r) represents the risk to public health if a PS bloom is not detected and responded to in a timely manner,

Response time (t) represents the total time involved in sample collection, shipping, and analyses plus, in the event of a confirmed outbreak, the time it takes to implement closure actions and to issue public warnings,

Monitoring (m) represents the extent of a PS monitoring program measured by the number of sample sites in an area and the frequency of sampling.

Equation (1) illustrates that the risk factor decreases with better monitoring or faster (i.e., reduced) response time. If the response time increases, the risk factor will become higher unless the delay could be compensated for by more intense monitoring. In remote areas where the logistics of sampling, transportation and the regulatory agency's ability to respond to sudden outbreaks preclude reasonable response time, it may be prudent to keep the areas closed. The risk equation implies that there is a point beyond which increases in monitoring effort may not adequately compensate for increases in the risk factor due to unacceptable lengthy response time.

Equation (1) assumes that the probability and intensity of an outbreak is uniform for any body of water. If one explores the hypotheses that some areas are more prone to PS blooms than the others, or that there may be cyclical patterns for PSP outbreaks, then it is possible to refine the risk assessment by incorporating historical data into the risk equation:

$$\text{Risk (r)} \propto \frac{\text{Response Time (t)}}{\text{Monitoring (m)}} \text{ X PSP Activity (A)} \qquad (2)$$

Where

PSP Activity (A) is derived from historic PS toxicity data in an area within a certain time frame. The PSP Activity is a macroscopic expression of the intensity and extensity of PSP outbreaks in an area (Chiang 1985).

At present, it is premature to introduce the PSP Activity parameter in risk assessment because most historic data in British Columbia were not obtained under a statistically defined sampling scheme.

PS Toxicity Monitoring

In British Columbia, the federal Department of Fisheries and Oceans monitors for the presence of paralytic toxins in shellfish. The monitoring program involves on-site sampling at key locations and verification sampling of commercial products at processing plants. Historically, fishery officers and patrol vessel crews sampled butter clams along an estimated coast line of 22,400 km (or 14,000 miles) in British Columbia. In 1960, there were 15 official sampling stations. The number increased to 46 in 1966 and by 1973, there were 56 stations. The sampling frequency of once every two weeks was targeted. The actual frequency varied, however, depending on the accessibility, the tide and the patrol schedule. In recent years, the successful deployment of mussel sampling stations provides an early warning system for PS blooms in key areas. Currently, the PS toxicity monitoring program in the Pacific Region consists of the following control points:

a) *Field Samples* are collected on-site by fishery officers and patrol crew from various beaches throughout the year. The sampling locations are based on modifications to the official list of the 1970's. In 1986, on-site samples collected by the Department accounted for 38% (638 samples) of the total number of 1696 samples. This component of the program provides the necessary data for closure or re-opening decisions. The ability of Departmental officials to respond quickly to sampling requests is a crucial factor in determining the size and extent of a closure.

To supplement the sampling data, shellfish growers and private citizens often assist in supplying on-site samples. Such samples accounted for 16% (or 270) of the 1986 total.

b) *Mussel Monitoring Stations* are set up during May to October at specific locations where commercial and recreational harvesting take place. The sampling is done under contract where local residents are paid a nominal fee for the collection of weekly samples from the monitoring stations. The samples are shipped collect to the Fish Inspection Laboratory. If the toxicity level at a particular station is high, the local fishery officer is alerted. The officer is also requested to collect on-site samples from the affected area to determine the extent of the toxic bloom. Area closure is immediately implemented if high levels are encountered. The tendency for mussels to accummulate PS toxins more rapidly than oysters or clams has proven crucial in providing the necessary lead time for added surveillances. The sensitivity of the mussel sampling program can be illustrated by the difference in PS toxicity levels found between the mussels and oysters in Okeover Inlet (Figure 1) and Sechelt Inlet (Figure 2). In 1986, all ten mussel sampling stations showed elevated toxin levels. Table 1 provides a list of the sampling stations in 1986. Samples from mussel monitoring stations accounted for 14% (or 243) of the 1986 total.

The Pacific experience has shown that sea mussels (Mytilus californianus) can be placed in a sock like net and submerged at an accessible location. Samples can be taken at any time independent of tide conditions. In locations where sea mussels are not normally found, stocks can be brought in and kept alive while suspended in the nets.

c) *Commercial Sampling* is conducted at certified shellfish processing plants by inspection officers. The frequency of sampling increases during the summer months to provide for greater consumer protection. It is important to note that commercial sampling serves mainly as a compliance verification measure to ensure that commercial shellfish are indeed safe. A toxicity monitoring program must not rely solely on commercial sampling. In 1986, there were 505 commercial samples taken, which accounted for 30% of the total.

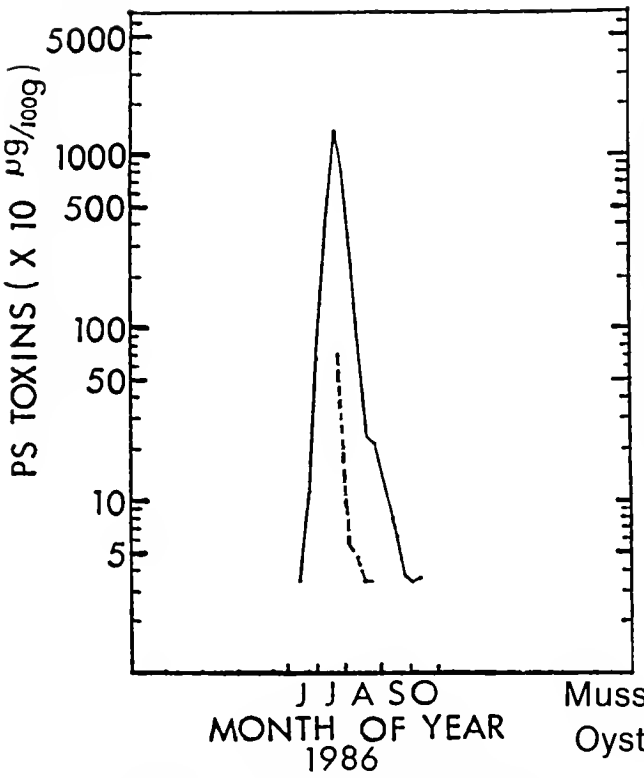

Figure 1. PS toxicity levels in Okeover Inlet.

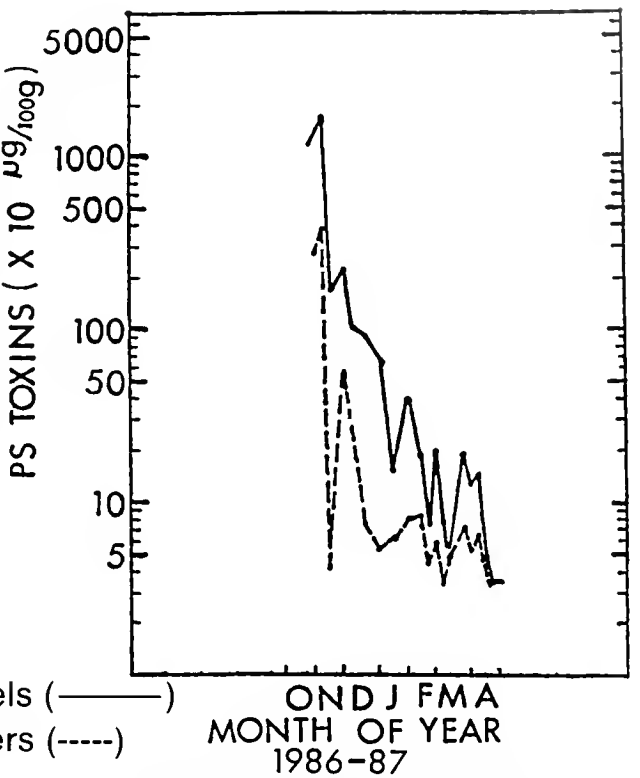

Figure 2. PS toxicity levels in Sechelt Inlet.

The Pacific program monitors for toxicity levels in the shellfish rather than the plankton species or the population dynamics of dinoflagellate blooms. Water samples are seldom taken for species identification or cell counts. Shellfish growers are, however, encouraged to conduct their own on-site monitoring. Plankton tows, turbidity examinations, water temperature and salinity studies are some of the basic tests that can be performed by the growers. Microscopic examination of the gills and digestive tract of the bivalve may reveal unusually high concentrations of single dinoflagellate species which signals bloom conditions.

Closure Decisions

It is internationally accepted that when the toxicity level exceeds 80 micrograms of toxin per 100 g of edible tissue, the area of harvest shall be closed and the product rejected. The decision to close an area is never easy. The spontaneous nature of toxic dinoflagellate blooms seldom afford decision makers the luxury of delineating closure boundaries that encompass the toxic area exactly. By the time sample results are known, the data could be out dated. A toxic bloom may be extensive or sporadic, thus affecting massive areas or only spotty locations. The intensity of a bloom may also vary, resulting in significant differences in toxicity levels among bivalves of the same or different species. The decision to close an area should therefore involve not only the 80 microgram criterium, but also the dynamics of the bloom. A good monitoring program may provide insights to the intensity and the extensiveness of a bloom. It may also indicate whether the bloom is active or subsiding. In the absence of perfect information, it is prudent, however, to include a sizable safety zone in the closure of an affected area.

Communication and Response

An effective communication system is important for rapid deployment of closure information. The industry and the public must be alerted with minimal delay. A telex is

TABLE 1.

Mussel monitoring stations in 1986.

Fishery statistical area	Location
13	Heriot Bay
14	Comox
15	Okeover Inlet
15	Lund
16	Egmont
16	Pender Harbour
17	Departure Bay
20	Point-No-Point
23	Sproat Bay
28	Whytecliff

issued from the regional headquarters to all fishery offices and industry subscribers of the telex system warning them of the closure. Fishery officers in charge of the affected area will prepare the necessary legal documents and advise local news media of the closure. Signs are posted to warn the public. Marine weather radio stations will also assist in alerting boaters in the affected area of the new closure. Inspection officers will contact shellfish processors to warn them of the closure. Product recently received from the affected area will be detained and sampled.

Enforcement

Closed areas are patrolled and enforced. Surveillance and enforcement action is an essential component of an effective shellfish management program. The Department of Fisheries and Oceans is responsible for the management of fisheries in Canadian waters. Enforcement activities are carried out under the auspices of the Fisheries Branch. A simplified organization chart delineating the functional relationship of enforcement activities among the different branches is illustrated in Figure 3.

Re-opening of Closed Areas

As soon as the closure announcement is made, the pressure to re-open an area begins to mount. A plan to increase the sampling of adjacent open areas should first be considered. If the results from the adjacent areas are negative, and existing data from the closed area show a subsiding trend, survey samples from the closed area may be considered. If consecutive samples from the same locations show accept-

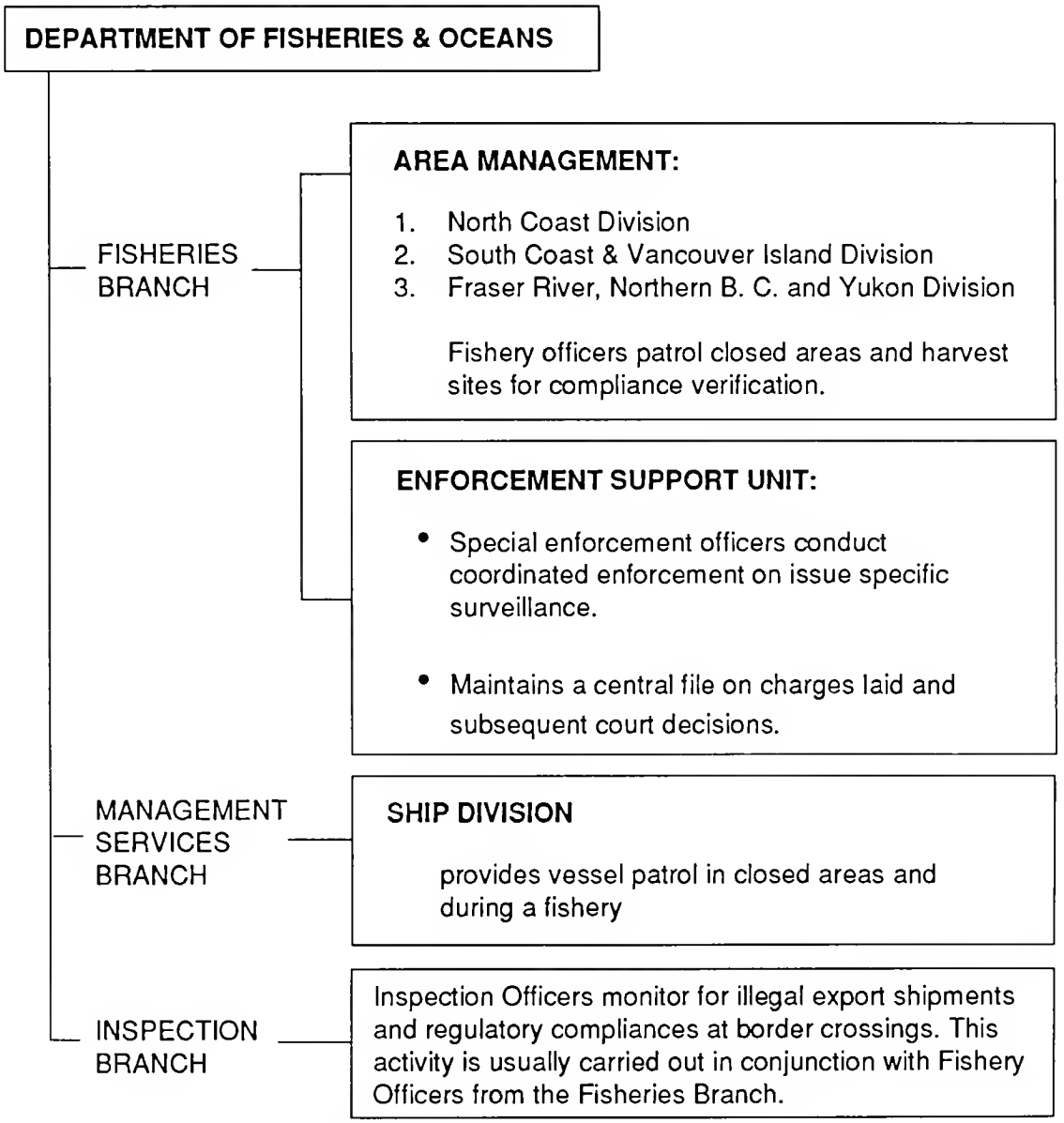

Figure 3. Organization chart for enforcement functions.

able results thus indicating a stabilized trend, the closure boundary may be reduced. Species with long toxicity retention time should, however, remain on the closure list.

DISCUSSION

Controllability

The essence of a shellfish program is controllability. It is known that toxicity levels can vary significantly among individual clams dug from the same beach at the same time. Quayle (1969) has reported that the toxicity levels of 41 individual butter clams so harvested had a range of 50–1568 ug. The mean was 669 ug with a standard deviation of 340 ug. Given the high variability of toxicity levels among individual clams and the sporadic nature of PS blooms, a PS toxicity management program must focus on the ABILITY to detect toxic blooms or bloom conditions in a body of water. This requires on-site monitoring samples be taken at regular intervals. In the absence of such data, lot by lot analyses of commercial products will not provide the same degree of safety confidence because product homogeneity cannot be assumed. Areas open to bivalve harvesting must therefore be monitored.

This approach is analogous to the sanitary growing water requirements where the harvesting of shellfish is permitted only in approved areas.

Program Effectiveness

There are different ways to verify the effectiveness of a PS management program. One approach would measure the percentage of commercial samples showing toxic levels in excess of 80 ug/100 g. In recent years, the percentages were 1%, 1% and 6% respectively for 1984, 85, and 86. Another measurement would involve the number of confirmed illnesses resulted from the consumption of toxic bivalves harvested in open areas. In British Columbia the number of such incidents are rare. Other than the 1972 outbreak in Barkley Sound which involved 10 illnesses from commercial clams, all other confirmed cases were resulted from recreational harvesting. Based on the incidents described by Quayle (1969), and departmental records on subsequent PSP outbreaks, a summary of PSP incidents in British Columbia from 1793–1987 is presented in Table 2. Of the 18 incidents recorded, there were 6 deaths and 113 illnesses. This method of body counting is, of course, unacceptable as a measure of program effectiveness—especially to those individuals who suffered the consequences.

Economic Considerations

The cost of a paralytic shellfish closure to the industry cannot be easily quantified (Conte 1984). The revenue foregone during a closure can be recaptured by the industry

TABLE 2.

Summary of PSP incidents in British Columbia, 1793–September 1987.

Year	Area	Location	Species/Toxicity ug/100 g	Comments
1793, June 15	7–7	Poison Cove, Mathieson Channel	Mussels	1 death, 3 sick
1942, May 2	23–7	Dodge Cove, Barkley Sound	Clams	1 death
May 3	23–11	Ucluelet, Barkley Sound	Mussels	2 deaths, 3 sick
1957, Oct 23	14	Comox, Baynes Sound	Oysters, Clams	34 sick, 23 sick
Oct 28			Mussels	4 sick
				7 cats died, 1 ill
1964,	5–14	Evinrude Passage, Angler Island	Butter Clams, 1168 µg	7 sick
1965,	15–4	Theodosia In.	Cockles, 1120 µg (Cooked)	1 death, 4 sick
1972, Nov 19	23–10	Toquart Bay	Manila Clams	2 sick (local)
			2100–4000 µg	10 sick (Seattle)
Nov 20	23	Ucluelet, Bamfield	Oysters, 1300–1900 µg	8 sick
1975, June 11	3–6	Work Channel	Mussels, 12,000 µg	2 sick
1980, May 16	12–39	Health Bay, Gilford Is.	Butter Clams, 8,600 µg	1 death, 7 sick
May 16	12–39	Shoal Harbour, Gilford Island	Butter Clams, 2,200 µg	3 sick
1981, Dec 17	13–18	Church House	Butter Clams, 2,400 µg	2 sick
				1 cat died, 1 ill
1982, May 30	3–6	Work Channel	Mussels, 30,000 µg,	5 sick
			14,000 ug (cooked)	
1985, May 8	12–38	Burdwood Group, N. of Gilford Is.	Littleneck Clams, 2,200 µg	4 sick
May 8	12–40	Bermingham Rock,	Bay Mussels, 5,000 µg	
		N. of Gilford Is.	Butter Clams, 9,600 µg	2 sick
1986, Oct 20	16–6	Sechelt Inlet	Bay Mussels, 11,000 µg	1 sick
1986, Nov 9	16–9	Sutton Is., Sechelt Inlet	Pink Scallops	1 sick
1987, April 21	17–6	Porter Beach, Chemainus	Butter Clam, 68 µg	1 sick
			(on medication at the time of consumption)	
				1 cat died, 1 ill

when the area re-opens, provided that product demand is re-established. Individual harvesters will suffer the loss of employment during the closure. The resources however, will not disappear but remain available upon lifting of the closure. Product demand is strongly influenced by consumer perception. If regulatory authorities can demonstrate that effective measures have been taken to contain the problem, and such measures are fully supported by the industry, the integrity of the bivalve mollusc fishery can be maintained and consumer confidence re-established quickly. While economists might debate the finer points of opportunity costs, the postponement of income to the industry represents the most significant impact of a PSP closure.

Decisions to open remote areas must give careful considerations to the risk factor and the cost of monitoring. Even if the regulatory agency has the capability to respond to sudden toxicity outbreaks without prolonged delays, the cost of monitoring may still be too high to offset any potential or short term economic gain. Seasonal openings during a low risk period may be the only practical solution for remote areas.

The sheltered inlets and uncontaminated waters of British Columbia offer tremendous opportunities for shellfish mariculture. To actualize this vast potential, coordinated development of remote aquaculture sites within reasonable proximity to each other will reduce the cost and enhance the effectiveness of a toxicity monitoring program. Productivity increases will enhance the benefit to cost ratio of servicing the industry.

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PARALYTIC SHELLFISH POISONING IN MAINE: MONITORING A MONSTER

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INTRODUCTION

Blooms of the toxic dinoflagellate, *Protogonyaulax tamarensis*, are a common, seasonal occurrence in the Gulf of Maine. Shellfish (e.g., mussels, clams, oysters, scallops) can accumulate the toxins produced by *P. tamarensis* rendering them vectors of paralytic shellfish poisoning (PSP).

Outbreaks of PSP present a problem with respect to optimal utilization of the shellfish resource as well as public safety. Magnitude of the economic losses is large, ranging from catastrophes (e.g., New England, 1972) and an estimated loss in excess of $7,000,000 in Maine in 1980 to the recurrent costs associated with the preventative shellfish monitoring programs.

Maine has established a comprehensive sampling program that has expanded over the years to accomodate the rising value of the resource (see Figure 1; Table 1) and the expansion of the species of shellfish utilized. Maine has the largest PSP monitoring/testing program in the country with approximately 3500 samples being run annually. This number, too, increases with the increasing number of areas affected.

In this paper we describe the monitoring program from its initial efforts to determine toxicity levels of shellfish to current efforts to effectively manage a resource in the presence of a potentially lethal phenomena. In addition, data are presented on detoxification studies in *Placopecten magellanicus* and their implications discussed.

HISTORY

The monitoring of shellfish as potential vectors for paralytic shellfish poisoning (PSP) and closure of shellfishing areas began in Maine in 1958. Following a serious outbreak of PSP in nearby Canada in 1957, five monitoring sites were established in this eastern Maine area. Closures were made in portions of this area in 1958, 1959, 1961, 1964, 1969, 1970 and 1972 whenever scores exceeded 80 μg of toxin. This limited monitoring plan, coupled with state of the art knowledge of the monitoring results in nearby Canada, provided adequate public health protection in eastern Maine. Prior to 1972, only occasional testing of the entire coast was conducted. This expanded sampling in 1961 resulted in two permanently closed areas around Matinicus and Monhegan Islands. Until 1972, no other areas were closed, although occasional low toxin scores were noted. In 1972, there was a closure in early August in eastern Maine.

In mid-September of 1972, it became evident that there were extremely toxic shellfish from Cape Ann, Massachusetts into western Maine. The aftermath of this discovery was the closure on September 15, 1972 from Cape Elizabeth to New Hampshire followed by closure of the entire coast on September 17th. Most of the coast, with the exception of Cape Elizabeth to New Hampshire, was reopened on September 30, 1972. Much of the area remained closed into 1973.

1973 did not require any new closures other than the historical area in eastern Maine; however, 1974, was a year of high toxicity. In the absence at that time of a precise sampling plan, it was a year of multiple crises. Although the laboratory was able to keep up with these crises, this 'shot-gun' method of monitoring toxicity levels can not be considered as a responsible public health protection program. Further, the lack of precise knowledge as to the areas which were toxic led to unnecessarily large areas being closed in order to give adequate public health protection.

Late in 1974, funding was obtained from the New England Regional Commission (NERCOM) to develop a monitoring program and to investigate the possibilities for the depuration of toxic shellfish. Work carried out under this contract was directed towards finding ways to reduce the impact of toxic dinoflagellate blooms on the shellfish industry of Maine. A greatly expanded monitoring program was implemented so as to provide more precise information about the temporal and spatial distribution of toxicity during bloom periods. To this end, 119 sampling stations were established along the coast of Maine.

The monitoring program at that time consisted of a series of 18 primary, 35 secondary, and 63 tertiary sampling stations. These were established on the basis of previous data. Primary stations were sampled on a weekly basis throughout the peak period of toxicity, i.e. April–October. Primary sampling stations were those which, in the past, were shown to be good indicators of the presence of toxins when present at low levels. Once toxicity was established at a primary sampling station, samples were taken at secondary and tertiary sampling locations. Secondary sampling stations were chosen on the basis of past results, as good indicators of what might be expected to

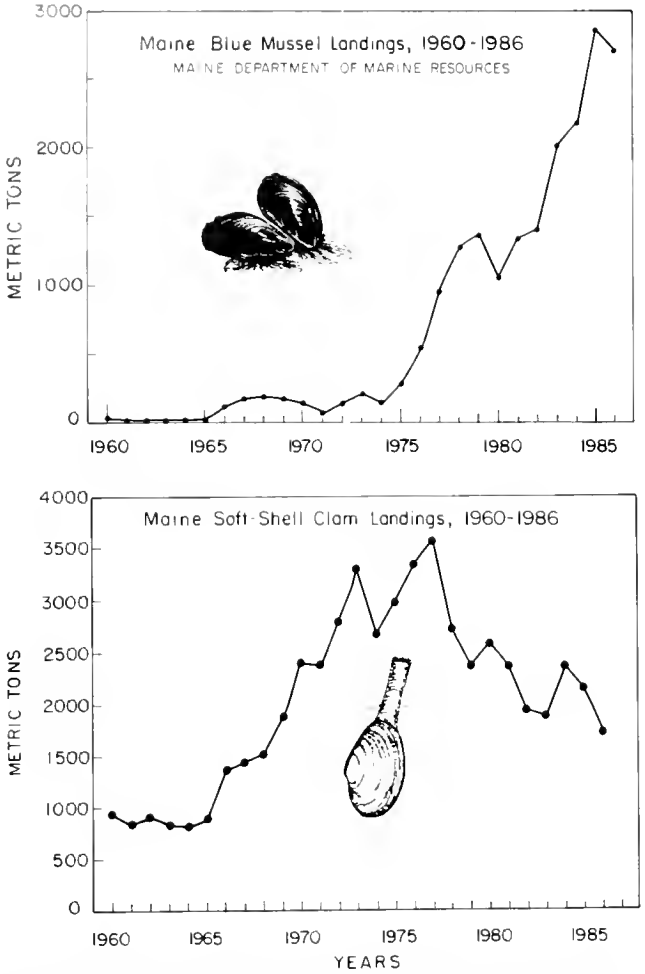

Figure 1. Landings data for the blue mussel, *Mytilus edulis*, and the soft-shelled clam, *Mya arenaria*, in the State of Maine from 1960–1986.

occur in a given clam growing area. Tertiary stations were chosen to fill in the gaps between the secondary sampling locations and to further localize the distribution of toxic areas. It was then, as it is now, the goal of the program to provide a safe method of monitoring the coast to ensure public health safety while at the same time causing the least disruption to harvesting activities.

Current Monitoring Procedures and Modifications

Years of practical experience have afforded us the opportunity to continually modify the sampling program. Presently, we instead consider areas. The coast of Maine is divided into 18 different areas from southwest to northeast with Area 10 the most southerly and area 27 in Cobscook Bay, the most northerly (Figure 2, Table 2).

At the beginning of the PSP testing year, we collect shellfish samples (mussels, *Mytilus edulis*, and clams, *Mya arenaria*) from each of these areas to determine the background level of toxicity (hopefully below quarantine levels). Four or five stations are sampled per area, usually

TABLE 1.

Maine landings of selected bivalve mollusks.

Year	Scallop	Clam	Mussel	Quahog	Oyster	Total
			(Thousands of Bushels)			
1980	539	378	155	?	1.0	1073.0
1981	639	346	197	1	1.1	1181.1
1982	266	452	208	7	3.1	936.1
1983	329	382	299	27	2.3	1039.3
1984	269	347	289	30	2.5	937.5
1985	135	317	406	38	5.1	901.1
1986	121	252	440	98	45	956.0
			(Thousands of Dollars)			
Year	Scallop	Clam	Mussel	Quahog	Oyster	Total
1980	10,752	8,554	546	?	62	19,914
1981	15,246	8,409	852	15	69	24,591
1982	6,295	10,236	903	98	200	17,732
1983	10,881	10,040	1,408	450	152	22,931
1984	9,437	11,606	1,668	510	168	23,389
1985	4,523	12,132	2,079	684	383	19,801
1986	4,160	12,300	2,319	1,960	3,600	24,339

including the original 'primary' station. These 'base' stations are sampled each week from April–October regardless of toxicity patterns. They are set up based on our historical information (and general trends) so that a closure can be made and the area described without having to return and resample the area before making the decision. A large part of the success of our progam is based on the speed at which a closure can be made. When the shellfish show toxicity, we expand our sampling, from the points of land inshore, until we find stations of little or no toxicity. With more expanded sampling, we can adequately describe toxic areas. This relatively heavy sampling concept has allowed us to manage around PSP closures, e.g., Casco Bay in 1979.

In 1979, using the information derived from our sampling program, we were able for the first time as a part of our management plan, to keep open a portion of the area, with the exception of mussels, which would have normally been closed for all shellfishing. This entailed a heavy-handed sampling program. Although the growing area which we sampled intensively was relatively small, during the 55 day closure approximately 155 shellfish diggers harvested 17,050 bushels of soft-shelled clams with a landed value of $426,250 and an estimated consumer value of $2,770,625 (Maine DMR).

Another area which we have been able to manage successfully is Cobscook Bay. By examining our extensive data base, we selected potentially safe areas. These areas are sampled twice a week throughout the extent of the potential problem. As the demand increases, we can develop more areas that can be similary managed.

Mussels, *M. edulis*, are our best prospect as an "alert" species and at the present time are they are being used as

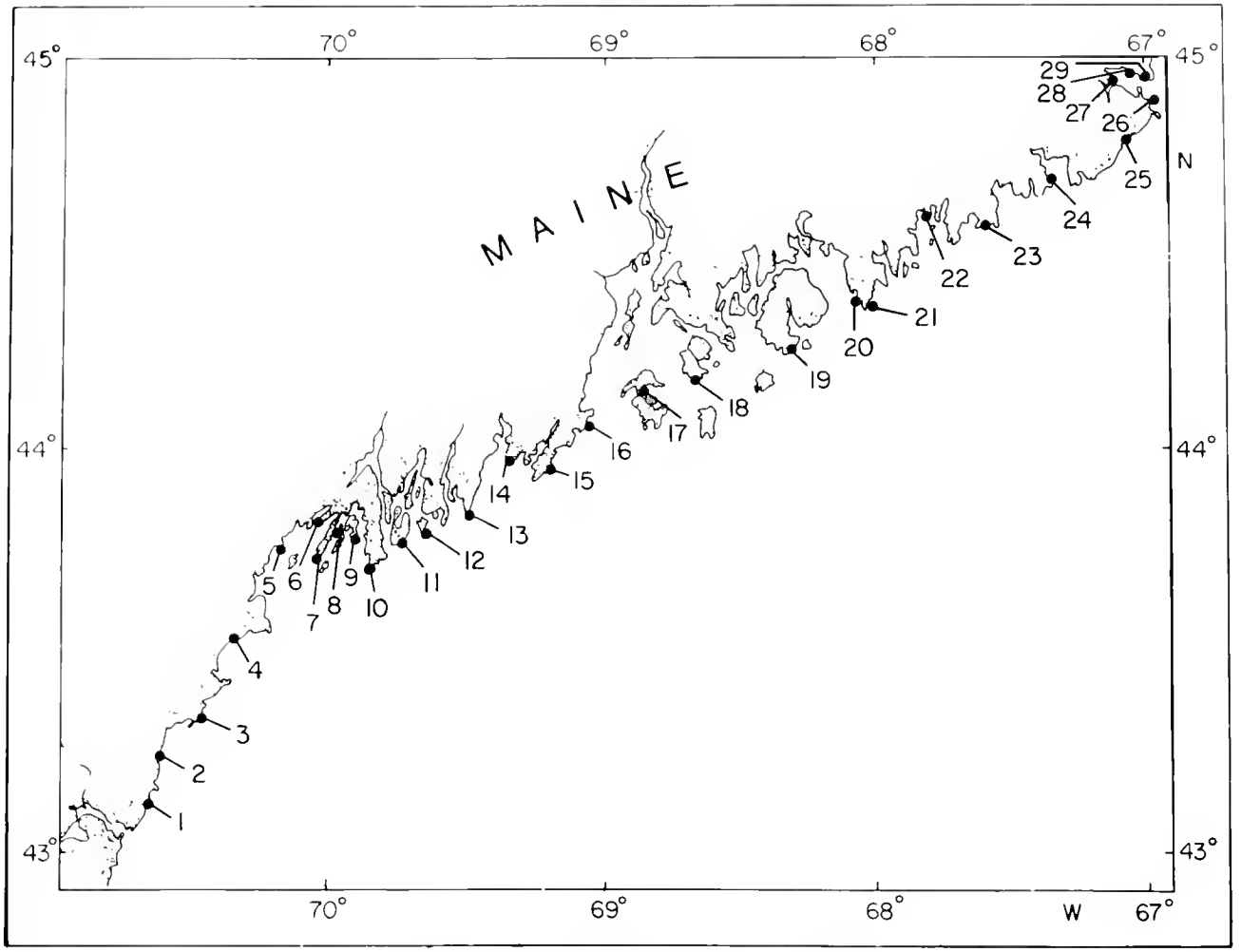

Figure 2. PSP sampling stations along the coast of Maine.

such. They become toxic approximately one week before *Mya arenaria* (Hurst and Gilfillan 1975, Shumway and Cucci 1987). With the recent risk in the harvesting of *M. edulis* and its gaining popularity (see Figure 1) as an inexpensive substitute for the soft-shelled clam, we take a greater risk of toxic shellfish on the market. Further expansion of our mussel sampling, possibly to the offshore islands, could give us a better early warning. Rises of toxin level in *M. edulis* and *Modiolus modiolus* have occurred without apparent alert. The best example of this is demonstrated by a rise in toxicity at Pemaquid Point in August of 1980 where routine sampling saw toxin levels at detection level rise to 8000+ $\mu g \cdot 100g^{-1}$ in two days (Figure 3). This rise resulted in the prohibiting of harvesting of mussels coastwide. Regular sampling offshore may help us to avoid this in the future or at least give warning.

In addition, winter sediment samples have been collected since 1980 along the coast of Maine for determination of the distribution of the resting cyst stage of *P. tamarensis*. The patterns of cyst distribution generally follow those of toxicity shown in Figures 4 and 5, but are not reliable as a predictive index for increases in shellfish toxicity (Thayer et al. 1983). Greater concentrations of cysts are also found in deep water sediments off the coast of Maine (Dale et al. 1978) than in the inshore waters. The direct role of the resting cyst stage in shellfish toxification is still being evaluated.

One thing that is evident from our records is the "PSP sandwich", the area of the mid-coast that is relatively free from the toxic dinoflagellate, beginning at the west side of Penobscot Bay extending northeast to Mt. Desert Island and beyond (Figures 4 and 5).

Maine imposes shellfish closures whenever toxin levels reach 80 $\mu g \cdot 100g^{-1}$. While it is theoretically possible to suffer poisoning from eating shellfish with low toxicity scores, there is no evidence that shellfish up to 80 $\mu g \cdot 100g^{-1}$ toxicity are unsafe. The available evidence indicates that the current quarantine level gives a significant safety factor as yet undefined.

Unlike Canada where the 'key' early warning monitoring stations are in areas closed for shellfishing year round, Maine's 'key' stations are adjacent to the principal

TABLE 2.

Locations of Sampling Stations (see Figure 2).

Station Number	Location
1.	York River (York)
2.	Ogunquit River (Ogunquit)
3.	Cape Porpoise (Kennebunkport)
4.	Spurwink River (Scarborough)
5.	Littlejohns Bridge (Cousins Is., Yarmouth)
6.	Mere Point (Brunswick)
7.	Potts Point (So. Harpswell)
8.	Lumbos Hole (Orrs Is. Harpswell)
9.	Cundys Harbor (E. Harpswell)
10.	Head Beach (Phippsburg)
11.	Little River (Georgetown)
12.	Newagen (Boothbay Area)
13.	Pemaquid Point (Bristol Area)
14.	Garrison Island Bar (Friendship)
15.	Port Clyde
16.	Spruce Head
17.	Vinalhaven Island
18.	Stonington (Deer Isle)
19.	Bass Harbor (Mount Desert Island)
20.	Mosquito Harbor (Winter Harbor)
21.	East Pond Cove (Schoodic Point)
22.	Ray Point (Milbridge)
23.	Henry Point (Jonesport)
24.	Starboard Island Bar (Machiasport)
25.	Moose River (Trescott)
26.	Lubec Channel
27.	Halowell Island (Whiting)
28.	Leighton Point (Pembroke)
29.	Perry-Eastport Causeway

shellfish harvest areas. Canada's experience indicates that a rise in toxin levels in clams at a key station will give, in most years, approximately a ten day warning of an expected increase in toxin levels in their principal shellfish areas. This toxin increase can be regarded as a significant 'alert' warning which allows safe management and planning of monitoring.

In Maine, the spring season mussels become toxic approximately one week prior to a rise of toxin in clams. Thus, mussel toxin levels present a fairly reliable prediction of a rise of toxin levels in clams. During fall blooms, rises of toxin levels in mussels have been observed over a period of 1–2 tides. This sharp rise in toxin has led to the speculation that an alert toxin level should be established below 80 $\mu g \cdot 100g^{-1}$. As an alternative for an alert toxin level, Maine has opted for critical observation of the mice for low level toxin reactions. This subjective observation takes considerable experience and is not a good substitute for a defined alert level which can be noted by anyone. The mouse bioassay is not sensitive enough to give reliable low toxin levels thus a substitute testing method such as high performance liquid chromotography (HPLC) must be used. With Maine's intense monitoring in place, whether an alert level below 80 $\mu g \cdot 100g^{-1}$ would add significantly to a public safety monitoring plans remains to be seen.

***Toxicity in scallops,* Placopecten magellanicus**

There has been a continued interest in developing an economic use for the discarded portion of scallops, the so-

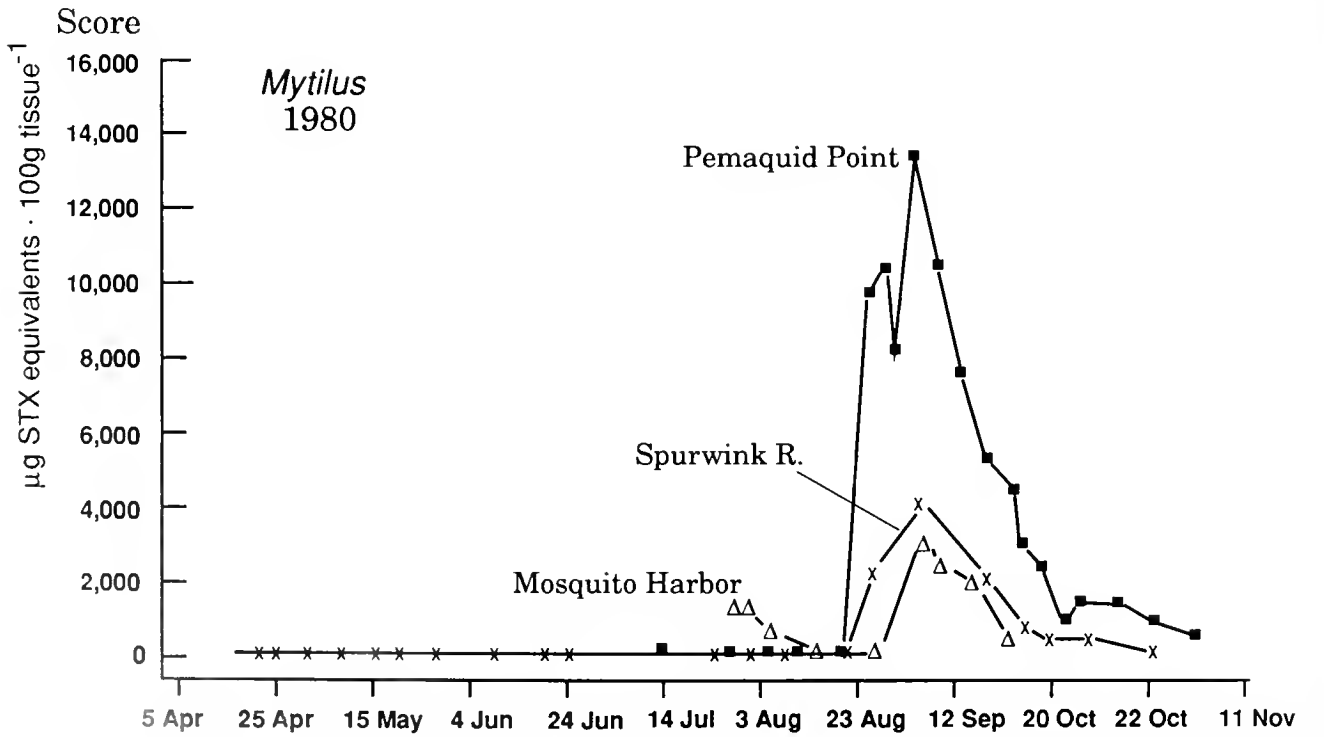

Figure 3. Toxicity levels (score) in µg toxin 100 g tissue^{-1} for the blue mussel, *Mytilus edulis*, from various localities on the Maine coast.

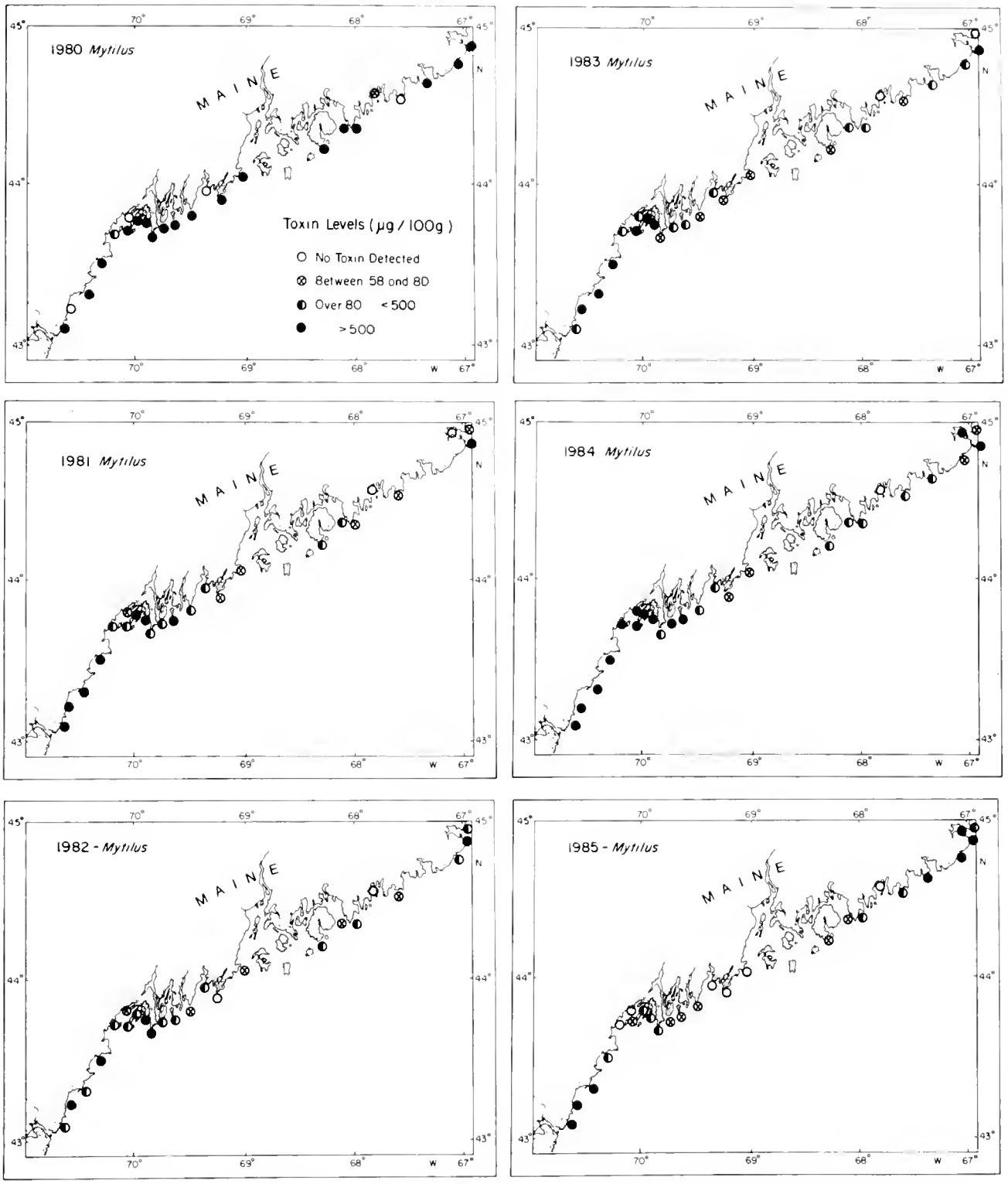

Figure 4. Toxin levels for the blue mussel, *Mytilus edulis*, along the coast of Maine from 1980–1985.

called 'rings and roes' (Bourne and Read 1965, Dewar et al. 1971). These tissues are comprised of the mantle, gonad, gill and digestive glands and can constitute weights equal to that of the excised adductor muscles. While there are several factors which have precluded the use of these parts (e.g., keeping quality, market acceptability), the most prevalent problem in New England and Canadian waters is the accumulation of neurotoxins derived from dinoflagellates, i.e., *Protogonyaulax tamarensis*.

A number of authors have reported on the levels of tox-

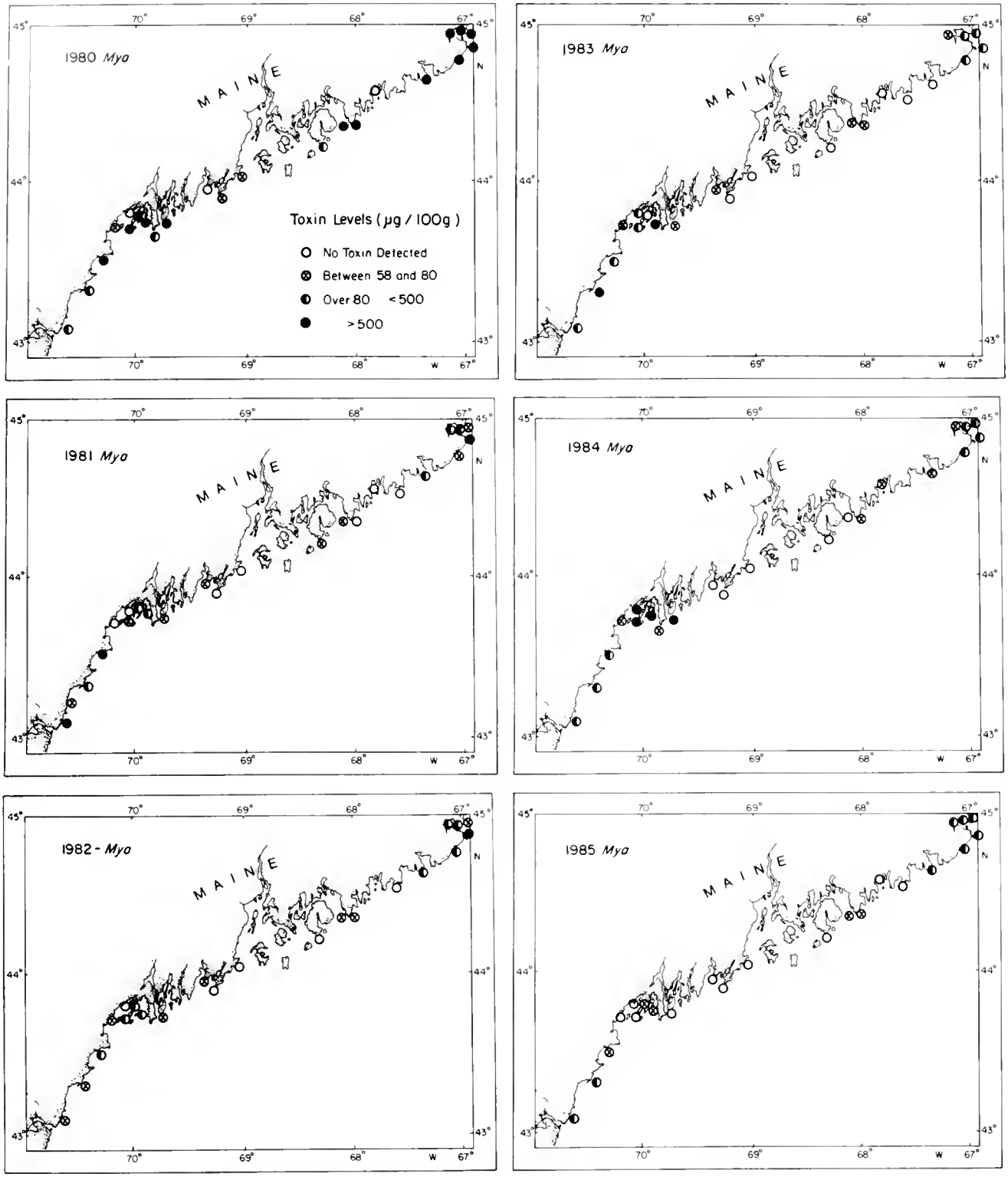

Figure 5. Toxin levels for the soft-shelled clam, *Mya arenaria*, along the coast of Maine from 1980–1985.

icity of various scallop tissues (Bourne 1965, Hsu et al. 1979, Shimizu and Yoshioka 1980, Noguchi et al. 1981, Ogata et al. 1982, Ueda et al. 1982, Jamieson and Chandler 1983) and a number of generalities have emerged:

1. The adductor muscle does not accumulate toxins and has, in fact, been shown to inactivate the toxins when present (Shimizu and Yoshioka, 1980). One exception has been reported in the purple-hinged scallop, *Hinnites giganteus*, where toxin levels reached 2000 µg · 100 g tissue^{-1} (Anonymous 1980).
2. Digestive gland, mantle, gonad and gill tissues all

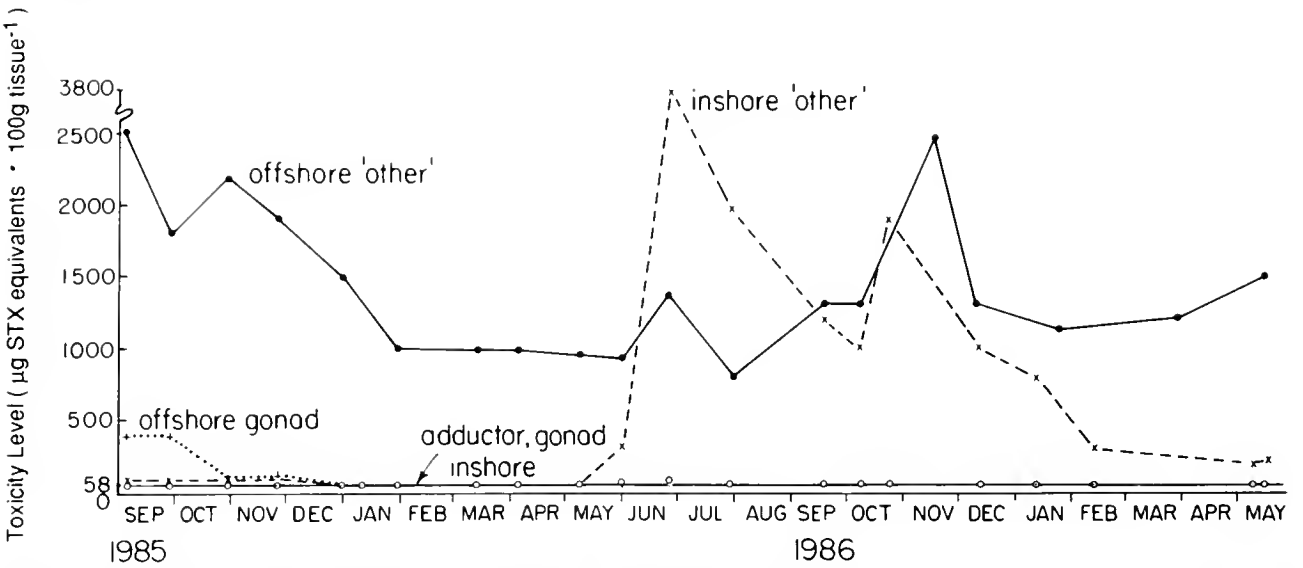

Figure 6. Toxicity levels of scallops, *Placopecten magellanicus*, from inshore (~30 m depth) and offshore (~150 m) collection sites. Data are given for gonad, adductor muscle and 'other' (including mantle gills and digestive glands).

retain the toxins although the levels vary between tissues and between species (Ueda et al. 1982, Jamieson and Chandler 1983, Bourne 1964, Medcof et al. 1947),

3. There are seasonal variations in toxicity level of the various tissues (Bourne 1965, Jamieson and Chandler 1983).

A recent renewed interest in trying to market not only scallop meats with roes attached, but whole scallops, has prompted further investigation in our laboratory regarding the seasonal distribution of toxin levels in the various tissues of the giant scallop, *Placopecten magellanicus*. Our results are given in Figure 6. Gonad tissues from inshore scallops were only toxic during May and June of 1988. The remaining tissue (digestive gland, mantle and gill) was toxic from September–November of 1985, May–December of 1986 and January–May of 1987. Scallops from offshore areas showed consistently high levels of toxicity in the 'other tissue' and high levels of toxicity in the gonads in September and November of 1985. These findings are similar to those of Bourne (1965) who demonstrated seasonal fluctuations in toxicity levels of the livers (digestive glands) and mantles of *P. magellanicus* from the Canadian east coast. Jamieson and Chandler (1983) also demonstrated seasonal variations in toxicity levels with peak toxicities occurring during fall and winter months.

Two interesting points emerge from our data. First, the scallops from the inshore water demonstrated high levels of toxicity even during periods when blooms were not evident. Second, the scallops collected from offshore areas (depths greater than 180 m) remained toxic throughout the year and showed some of the highest levels recorded in our study. The source of toxin for these deep water scallops is not clear. Bourne (1965) first suggested the possibility that scallop toxicity could be caused by the resting cyst stage of *P. tamarensis*. These cysts are present in sediment samples and have been shown to be considerably more toxic than their motile cell counterparts. This possibility was later suggested again by Yentsch and Mague (1979) and Jamieson and Chandler (1983). Data available on the distribution and abundance of cysts (Lewis et al. 1979, White and Lewis 1982, Thayer and Lewis 1983) suggest that there is a broad distribution of cysts, sometimes in high densities, in the sediments off the Coast of Maine and in the Bay of Fundy. However, the abundance of cysts in locations of commercial scallop beds has been shown to be low (Sherman-Caswell unpublished). More recently, Anderson (1984) argued that a scallop would require consumption of as many as 100 million cysts to achieve the toxin levels recorded in deep water scallops! He recommended caution in assigning toxic events to cyst ingestion and our results support his skepticism. In our most toxic individuals (>1500 µg · $100g^{-1}$), careful examinations were made to identify and count the cysts present in the guts. In no instance could we locate any cysts. Further, in a series of experiments to determine the time necessary for these scallops to detoxify, we found that after a period of 4 months, toxicity levels had only decreased by approximately one third (Figure 7).

We suggest that the toxicity observed in the deep water scallops may be due to the ingestion of raining cells of *P. tamarensis* during the bloom period (early spring and fall) and the consequent slow rate of detoxification. It is also possible that the scallops transform the toxins and store them from one season to the next.

Our results, along with those of previous authors, suggests that the gonad tissue of *P. magellanicus* could be safely marketed from most geographic locations tested. Caution should still be observed and frequent sampling for toxin levels should be maintained. We strongly caution

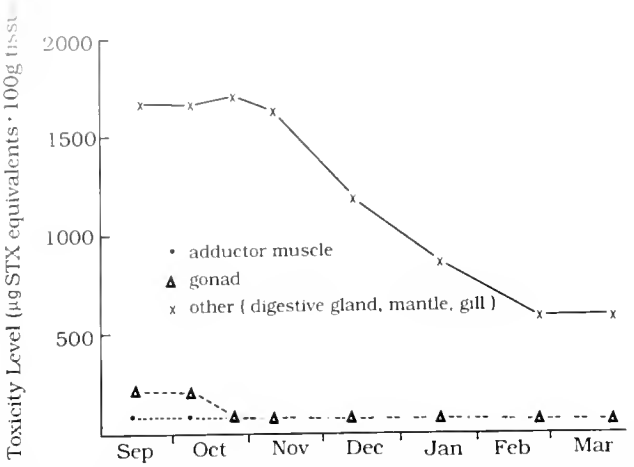

Figure 7. Toxicity levels of scallop tissues (*Placopecten magellanicus*) during detoxification. Animals were placed in filtered, running sea water at the beginning of the experiment (September) and maintained under these conditions through March.

against the marketing of whole scallops from any area of the coast of Maine or Canada due to the high levels of toxins recorded from digestive glands and other tissues and to the unpredictable seasonal variation in those toxin levels.

***Toxicity in ocean quahogs*, Arctica islandica**

In 1985, we began more intensive screening of the ocean quahog, *Arctica islandica*, for paralytic shellfish toxins. The quahog fishery is relatively new with the majority of harvesting done around the Jonesport and Machias Bay areas. Around late August, there was a significant rise in the toxicity level of these shellfish. Prior to this period, only low levels of toxin had been detected. Samples taken from commercial dealers showed levels well over quarantine, with a maximum of 1895 $\mu g \cdot 100g^{-1}$ in August. Quahogs remained toxic into October. Sampling stations off of Jonesport (east and south) and Machias Bay, remained toxic through the spring of 1986 with levels ranging from 80–532 $\mu g \cdot 100g^{-1}$. The area from the Jonesport-Beals Bridge to the International Border (seaward to the U.S. jurisdiction was closed to the harvesting of ocean quahogs on August 6, 1985. After samples of quahogs were tested as safe, a portion of these waters, Machias Bay and inshore of a line from Jonesport to Cutler, were reopened. A part of this closure still remains in effect.

The source of the toxin for these quahogs has yet to be determined although the original rise in toxicity in late August was also seen in blue mussels, *M. edulis*, at Starboard Island Bar, Point of Maine, Jonesport, which lies adjacent to the quahog beds as seen in Figure 8. Soft-shelled clams, *Mya arenaria* from the same area also showed a rise in toxin level during that period although not as severe. Other stations in the Machias area did not reflect the rise at that time. Further east at Lubec, West Quoddy Bar and Cobscook Bay, evidence was seen of a 'fall' bloom of *P. tamarensis*.

A clearer understanding of the mechanisms of intoxification of near and offshore subtidal species (e.g., *Arctica*, *Placopecten*) is needed. They do not seem to follow the patterns of intoxification that are seen in the intertidal species. Once understood, this knowledge could aid in developing a more effective management plan.

Due to a lack of historical data, it is only speculation that *M. edulis* at Starboard Island Bar and Lubec would serve as a warning of a rise of toxin in the quahogs. A more intense sampling program is needed to understand this problem. As the fishery expands to other parts of the Maine coast, more extensive sampling will also be needed to manage the resource.

***Toxicity in hen clams*, Spisula solidissima**

Regular testing of the surf or hen clam, *Spisula solidissima*, began in 1975. There is a small, bottom dredge fishery in southern Maine for these clams, which can also be harvested from the shores/beaches on the low drain spring tides. Eight sampling stations were established from Scarborough south to York with two stations in the Phippsburg/Georgetown area as well. These are sampled regularly throughout the year depending on the toxicity of the shellfish. *S. solidissima* has been shown to retain the toxins for over a year (Medcof et al. 1947, Blogoslowski and Stewart 1978, Shumway unpublished) and therefore these stations are sampled in the spring and summer each year and through the fall and winter months during years of toxicity. In 1980 and 1981, surf clams became quite toxic in some areas as seen in Table 3; Figure 9. The Maine coast from Georgetown to the New Hampshire border was closed to surf clams on October 1, 1980 and remained closed until May 2, 1981 when a portion between Pine Point, Scarborough and Fletchers Neck, Biddeford was opened, only to be closed again on May 29. This remained in effect until September 10, 1981, then the exception was included again and this closure remained until December 27, 1982. A large part of this closure can be accounted for by the sequestering of the toxin by these shellfish. The Higgins Beach station (Figure 9) stayed well over quarantine level for 2+ years from the initial bloom in 1980. There may have been some retoxification in the spring of 1981 as seen at Higgins Beach but Head Beach and Scarborough Beach reflect the slow depuration pattern seen in *S. solidissima*.

SUMMARY

Like other successful monitoring programs (see Chiang this volume), the objectives of the Maine PSP program are public safety and the optimum utilization of the resources. The frequent and intense sampling of growing/harvesting areas works well, prohibiting the taking of potentially toxic shellfish. Rapid implementation of closures avoids the costly problems associated with seizing commercial catches although closed areas must be patrolled frequently.

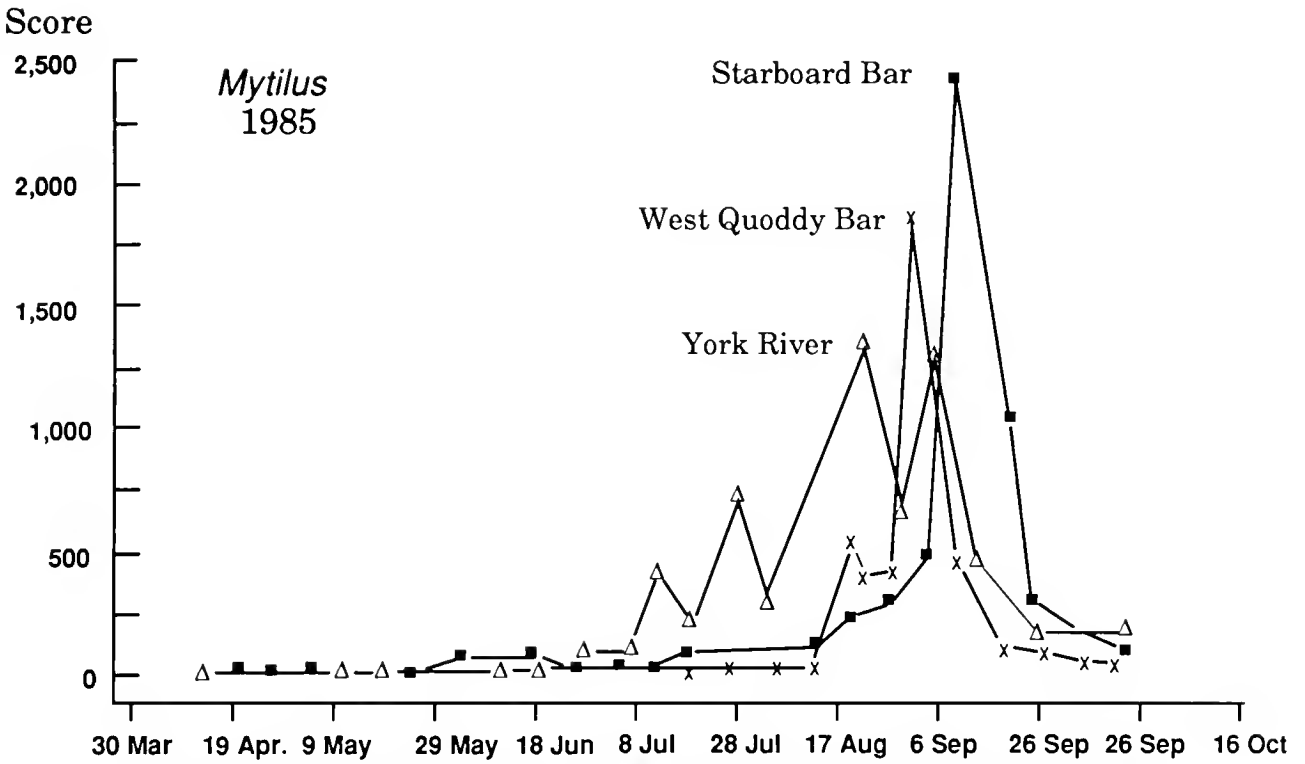

Figure 8. Toxicity levels (score) for the blue mussel, *Mytilus edulis*, from various localities on the Maine coast.

Further, the program should be in touch with the industry and aim for optimum use of the resources. It must be flexible enough to include new species entering the fishery, e.g., *Arctica islandica*, as well as account for new ways to utilize species already monitored, e.g., *Placopecten magellanicus*. Up to date knowlege of the shellfishing industry and its demands is required as the closures of large areas of the coast that are not species specific can be very costly. The program must be intensive and distinguish larger harvestable areas.

To be effective, a monitoring program not only should be intensive in its screening of shellfishing areas, but have a good early warning agent. Plankton samples can be collected fairly easily, but must be analyzed immediately to be of any help. This requires a large staff. In addition, total numbers of cells may not reflect the predicted toxicity of the shellfish (Cembella et al. 1987). Better sampling of offshore populations (e.g., *Mytilus*) could aid in early warning; it has been observed that the offshore islands can become toxic before the mainland (Maine DMR). This, too, requires a larger staff.

Finally an effective monitoring program must be flexible

TABLE 3.

Maximum Scores (μg · 100 g tissue^{-1}) for the surf clams, *Spisula solidissima*.

	1980	1981	1982	1983	1984	1985
Higgins Beach	4518	5316	612	193	244	<58
Scarborough		(viscera only)				
Scarborough Beach	1752	928	161	101	470	59
Pine Point Scarborough	91	64	<58	<58	<58	—
Old Orchard Beach	<58	<58	<58	<58	59	—
Moody Beach Wells	672	365	71	174	715	162
Ogunquit Beach	78	331	152	98	172	303
Long Sands York	—	90	—	—	—	179
Head Beach	4993	7934	557	202	690	64
Phippsburg		(viscera only)				
Sagadahoc Bay Georgetown	5104	202	87	69	68	<58

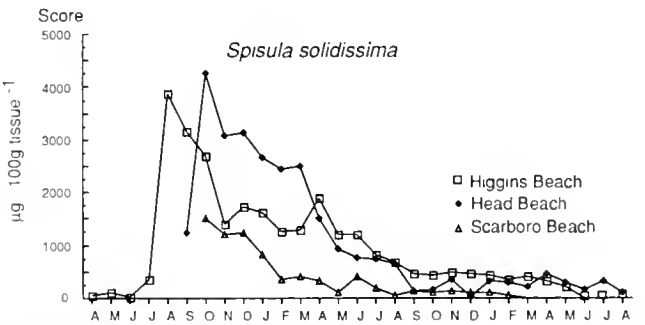

Figure 9. Toxicity levels (score) for the surf clam, *Spisula solidissima*, from various localities in Maine (1980–1982).

and able to handle day to day "emergencies" e.g., unexpected outbreaks of PSP or incidents such as the recent outbreaks of unidentified poison from Canadian waters.

The PSP monitoring program in Maine has grown continuously and is constantly being modified in an attempt to serve both the consuming public and the working industry. Economic losses due to rises in toxicity levels have been lessened. More importantly, no deaths or illnesses have been attributed to PSP from shellfish harvested in the State of Maine. All documented illnesses have resulted from recreational harvesting. This can only be corrected by increased public awareness. To this end, notices are posted that can be seen by land access to all closed areas. Shellfish dealers and towns involved are notified of all closures. Closure notices are published in newspapers and are announced on the weather broadcasting radio station. Finally, several articles (newspapers and magazines) have been written on the subject of toxic shellfish. The goal is to keep the public aware of their responsibility to use the resource wisely without seriously affecting the market for Maine shellfish and ensuring the safety of the product. The program has become more effective with time but there is always room for improvement.

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PSP TOXINS IN THE PACIFIC COAST STATES: MONITORING PROGRAMS AND EFFECTS ON BIVALVE INDUSTRIES

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ABSTRACT Recent changes in three inter-related factors are described for each of the four continental Pacific states: changes in the occurrences of high concentrations of PSP toxins in shellfish, changes in the bivalve industries, and changes in the PSP monitoring programs. From 1980 to 1987 in California and Oregon there was a fairly consistent occurrence of episodes in which recorded levels of PSP toxins in bivalves were higher than in the previous two decades. (Toxin values in Oregon were much lower than in California.) In Washington episodes with relatively higher toxin levels began in the early 1970's and continued through 1987. Available Alaska shellfish toxicity data does not date far enough back to permit such a comparison, but the number of episodes of PSP illnesses in humans has increased since the mid-1970's, indicating high levels of toxin in shellfish during that period. In all four states harvesting of wild bivalves and/or aquaculture has expanded in terms of the area involved and diversified in the number of species being harvested commercially, despite the increase in potential toxicity problems. This expansion of the industries has been made possible, in part, by increased monitoring for shellfish toxicity in all four states and by procedures for lot sampling in Washington and Alaska. The effects of PSP toxins on the bivalve industry range from delay of harvesting during short-term closures to destruction of an established fishery based on a species for which there are long-term or permanent harvesting closures. In some areas development of fisheries for new species may be precluded by the continued presence of toxins.

KEY WORDS: PSP, *Gonyaulax*, *Alexandrium*, *Protogonyaulax*, bivalve industry, monitoring program, Pacific states

INTRODUCTION

The Pacific coast of North America has a long record of paralytic shellfish poisoniong (PSP) episodes, dating back to the exploratory voyage of Captain Vancouver in 1793, when four men became ill and one died after eating mussels in what is now British Columbia. In 1799, 100 men of the Baranoff expedition died of PSP after eating mussels in Alaska (Quayle 1969). In California four episodes with 1–13 cases each between 1903 and 1918 (Halstead 1965) were followed by an episode with 103 cases with 6 deaths in 1927. This spurred mussel poisoning research during a series of California outbreaks in 1929 and the 1930's. The source of the toxin in mussels was identified as the dinoflagellate *Gonyaulax catenella* Whedon and Kofoid (Sommer et al. 1937). [Because there is lack of concurrence among taxonomists about two proposals to assign this species to a different genus, *Protogonyaulax* (Taylor 1979) or *Alexandrium* (Balech 1985), the original name is used in this paper.] A mouse biooassay to detect the toxin was developed (Sommer and Meyer 1937). PSP episodes have continued to occur with varying frequencies in British Columbia (Quayle 1965, Canada Department of Fisheries and Oceans 1984, 1985, 1986) and in the four continental states on the Pacific Coast (Table 1).

The monitoring programs of the four Pacific Coast states and the impact of PSP toxins on their bivalve industries have been described by Lutz and Incze (1979), Yentsch and Incze (1980) and Nevé and Reichardt (1984).

This paper describes three inter-related types of changes which have occurred in the last decade:

(1) Changes in species and areas of the commercial shellfisheries,
(2) Changes in the areas and frequencies of occurrence of high levels of PSP toxins in shellfish and the effect of the toxins on the industries,
(3) The resultant adjustments which the individual states have made in their efforts to prevent PSP, particularly in the shellfish monitoring programs.

The four states vary widely in the size, value, and species of their commercial bivalve shellfisheries (Table 2), the levels of toxicity reported (Table 3), and the modes of preventing PSP (evidenced in part by the sizes of their monitoring programs, Figure 1). Because of these variations, the changes in the bivalve industry, PSP occurrences, and public health protection will be described separately for each state.

CALIFORNIA

History of PSP Toxins in Shellfish

The coast of California has had more recorded cases of PSP than any of the other three Pacific Coast states, with 538 illnesses and 39 deaths reported through 1987 (Table 1). Following the major outbreaks in the 1920's and 1930's, the Department of Health in 1939 initiated a mussel quarantine which banned the taking of all species of mussels, except for fish bait, from May 1–October 31. The quarantine order has been re-issued each succeeding year. In 1962 a PSP monitoring program was initiated to provide added public health protection for the consumption of other native species and commercially produced oysters.

TABLE 1.

Reported occurrences of paralytic shellfish poisoning in California, Oregon, Washington, and Alaska, 1799–1987.

	California		Oregon		Washington		Alaska	
Year	Cases	Deaths	Cases	Deaths	Cases	Deaths	Cases	Deaths
1799							150+	100+ f
1903	12	5 a						
1915	4	a						
1917	13	2 a						
1918	1	a						
1927	103	6 b	many,	date? a				
1929	60	4 b						
1930	2	b						
1931	2	b						
1932	44	2 b						
1933	12	b	21	1 a				
1934							12	2 f
1936	3	2 b						
1937	27	b						
1938	3	b						
1939	76	8 b						
1942					several	3 a		
1943	20	4 b			2	a		
1944	12	2 b					4	1 f
1946	3	1 b						
1947	1	b					3, date?	1 f
1948	3	1 b						
1954	5	b					8	1 f
1962	4	b					27	1 f
1965							4	1 f
1969	15	b						
1970							2	f
1971	15	b					8	f
1973							4	f
1976							10	g
1977							17	g
1978					10	d		
1980	98	2 b					11	g
1981							18	g
1982			1	c			19	g
1983							6	h
1984							1	h
1985					2	e	6	j
1986							7	g
1987							7	g

a = Halstead 1965, b = Sharpe 1981, c = Arnold pers. comm., d = Washington Office of Public Health Laboratories and Epidemiology 1978, e = Cox pers. comm., f = Orth et al. 1975, g = Middaugh pers. comm., h = Middaugh 1985, j = Middaugh 1987a.

Evidence of the widespread and frequent occurrence of the toxins in shellfish is provided by the records of the monitoring program and by reports of illnesses prior to monitoring. Since 1962 toxin levels equal to or exceeding 80 μg toxin/100 g shellfish meat (the level set by U.S. Food and Drug Administration as the harvesting closure level) have occurred in all counties except Del Norte (Figure 2). (The lack of recorded closure levels there may be due in part to the fact that samples from that county are rarely submitted.) Prior to 1962 PSP illnesses had occurred in Del Norte County also, indicating that none of the coastline is exempt from outbreaks of shellfish toxicity (Sharpe 1981). Outbreaks in which toxin levels in shellfish have exceeded the closure level have been nearly annual events, having occurred in one or more locations in 23 of the past 26 years (Price, D. 1987, pers. comm.).

These records also demonstrate the enormous variations which have occurred in the intensity, geographical distribution, and timing of blooms of the toxin-producing dinoflagellate. The highest toxicity value (μg toxin/100 g shellfish meat) recorded during each year since 1962 varied from 61–16,000 μg (Table 3). In 10 of the 26 years of monitoring, toxicity levels exceeded 1000 μg. (1000 μg is considered a sufficient dose to cause severe PSP symptoms or,

TABLE 2.

A comparison of the weight and value of bivalves produced in California, Oregon, Washington, and Alaska in 1978 and 1986.

	Metric Tons							
	California[a]		Oregon[b]		Washington[c]		Alaska[d]	
	1978	1986	1978	1986	1978	1986	1978	1986
Oysters	465	514	119	148	2619	3960	—	—
Hardshell clams	—	—	98	38	1301	2726	—	8
Geoducks	—	—	—	—	3223	1297	—	60
Razor clams	—	—	19	1	161	32	36	125
Bay mussels	—	152	—	—	5	135	—	—
California mussels	—	—	<1	17	—	—	—	—
Pink scallops	—	—	—	—	—	20	—	—
	Thousands of Dollars							
Oysters	1,137	2,866	na	na	3,997	11,296	—	—
Hardshell clams	—	—	43	49	556	4,997	—	4
Geoducks	—	—	—	—	1,279	1,855	—	26
Razor clams	—	—	39	6	316	88	78	145
Bay mussels	—	268	—	—	11	349	—	—
California mussels	—	—	<1	33	—	—	—	—
Pink scallops	—	—	—	—	—	51	—	—
Totals	1,137	3,134	82+	88+	6,159	18,636	78	175

[a] California Department of Fish and Game 1987.
[b] Oyster data, Oregon Department of Agriculture 1987, weight estimated as 3.95 kg/gallon; data for other species, Oregon Department of Fish and Wildlife 1976–1986.
[c] Washington Department of Fisheries 1985, 1986.
[d] Alaska Department of Fish and Game 1976–1987.
na = data not currently available.

in some individuals, death; 100 g shellfish meat would be a moderate serving.) The locations of the highest values recorded during each year indicate the areas most frequently affected by the toxic blooms (Figure 2). In 18 of the 26 years since 1962 the location of the mussels with highest toxicity was within the 400 km section of the coast from Mendocino County to San Mateo County. In 12 of those 26 years (including 6 of the last 8) the highest values were found in Sonoma and Marin Counties (Price, D. 1987, pers. comm.).

The May 1–October 31 quarantine period, set in 1939, reflected information then available on timing of blooms, based on records of illnesses. However, monitoring data has shown that elevated levels of toxins occur in mussels at times other than the quarantine period. In the four southernmost counties toxicity values exceeding 80 μg are as likely to occur during November–April as in the quarantine period. Several unusual outbreaks of toxicity exceeding closure level have occurred in the non-quarantine period along the central coast also. The following toxin values were reported during November–April: 330 μg in November 1980 in Mendocino County, 240 μg in February 1970 in Sonoma County, 240 μg in March 1976 in Marin county, 4000 μg in March 1984 in Marin county (during a major bloom which necessitated closures from Sonoma to Santa Cruz Counties), and 4100 μg in April 1985 during another major bloom in the Santa Barbara area (Price, D. 1984, 1986).

Evidence that nearly all, if not all, major blooms originate in the ocean, not within bays, is found both in the variations in toxin levels along the coast and in a comparison of toxin values within bays with those on the open coast.

Prevention of PSP

The wide ranges in distribution, timing, and intensity of blooms point to the enormity of the task of protecting the public from PSP in this populous state with a climate conducive to high usage of the 1800 km of coastline. The Department of Health Services views PSP prevention as a 3-part program which includes the mussel quarantine as the basic means of protection, the monitoring program for information about toxin levels in other bivalve species, and a public education program for dissemination of information about both current conditions and general problems of shellfish and PSP.

The monitoring program is the responsibility of the Environmental Planning and Local Health Services Branch (EPLHSB) of the Department of Health Services. Commercial growers submit samples weekly year-round when harvesting. (In Pacific Coast states licensed bivalve producers harvest on large privately owned or leased state-land tracts, using hired diggers or dredges. Samples submitted for PSP testing are from the areas currently being harvested.) Shellfish samples from coastal locations, especially near popular sport-harvesting areas, are collected year-round, with an

TABLE 3.

Highest toxin values reported in any species of shellfish during each year, μg toxin/100 g shellfish meat.

Year	California[a]	Oregon[b]	Washington[c]	Alaska[d]
1957			346	
1958		359	795	
1959		0	148	
1960		—	532	
1961		—	373	
1962	1920	0	347	
1963	400	0	586	
1964	61	0	1032	
1965	340	0	1420	
1966	1600	0	365	
1967	240	16	518	
1968	270	—	252	
1969	2300	31	1090	
1970	2800	27	390	
1971	6000	0	242	
1972	131	46	1090	
1973	162	904	465	4550
1974	92	59	1080	na
1975	498	39	1370	na
1976	280	29	2220	6107
1977	66	0	605	na
1978	92	38	30360	na
1979	68	42	1310	na
1980	16000	121	2503	1760
1981	2200	149	3880	na
1982	690	1675	1751	5030
1983	240	44	2139	4793
1984	4000	415	2014	876
1985	4100	<36	1106	1021
1986	1900	<42	1635	5674
1987	500	113	1514	5855

[a] Rogers 1987.
[b] Oregon State Health Division 1958–1987.
[c] Washington Department of Social and Health Services 1957–1987.
[d] Alaska Department of Environmental Conservation 1981–1987.
na = data not available.

increase in sampling frequency during the May-October quarantine period. Coastal sampling is conducted by EPLHSB and a variety of volunteers, including county health departments, military bases, marine laboratories, Department of Fish and Game, and private individuals. EPLHSB encourages routine sampling of either the California mussel, *Mytilus californianus* (Conrad), or the bay mussel, *M. edulis* (Linnaeus). Sampling is expanded to other species as required during blooms.

Closure announcements and other information about PSP are issued to the news media by one agency, the Department of Health Services, to avoid multiple or confusing reports. Because many of the PSP patients have been new arrivals to this country with limited command of English, multilingual signs are posted at some closed beaches, and efforts have been made to provide PSP information to leaders of various ethnic communities. Monthly EPLHSB reports to the various health agencies and participants in the monitoring program provide current toxicity data and additional insight into potential PSP problems based on analysis of long-term data (Price, D. 1987, pers. comm.). Public education about PSP has been aided by the publication of a general information leaflet by California Sea Grant Program (Price, R. 1986).

The EPLHSB is concerned that the frequency and spacing of sampling on the open coast have been inadequate to protect recreational harvesters, particularly in the northern counties. Additional staffing beginning in 1988 will permit EPLHSB to rely less on voluntary sampling and will substantially increase the coverage of the monitoring program (Price, D. pers. comm.).

Effects of PSP Toxins on the Shellfish Industry

Historically the major commercial bivalve shellfish industry has consisted of culturing Pacific oysters (*Crassostrea gigas* Thunberg) in five bays, Humboldt, Tomales, and Morro Bays, Drakes Estero and Elkhorn Slough (Figure 2). In Tomales Bay small amounts of the European oyster (*Ostrea edulis* Linnaeus) and the Eastern oyster (*Crassostrea virginica* Gmelin) have been produced also. The oyster industry produced 753 metric tons (MT) (packed weight) in 1960, then underwent a decline in the late 1960's and much of the 1970's, and has rebuilt to the 570 MT level in 1984 (Figure 3) (California Department of Fish and Game 1987). In the last decade the bivalve industry has both diversified in terms of species grown and expanded into new areas. Commercial production of bay mussels has been added in Tomales Bay and Morro Bay. Operations in new locations include culture of Pacific and European oysters and bay mussels at Carlsbad, and European and Pacific oysters, scallops (*Pecten* spp.) rock scallops (*Hinnites multirugosus* Gale), and bay mussels in the Santa Barbara Channel area, the scallops and mussels being grown on offshore oil platforms (Price, D. pers. comm.). Statewide mussel production increased 3-fold from 1985–1986, to 152 MT. In 1987 there were 34 registered marine bivalve aquaculturists in California: 14 commercial producers of shellstock, 3 commercial producers of bivalve seed, and 17 aquaculturists registered for research and development or experimental cultivation. Of these, 12 are registered for cultivation of several species of clams (California Department of Fish and Game 1987). [The small commercial fishery of wild clams for human consumption, which existed in the early 1900's, declined and collapsed in 1965 because of pollution, overharvesting, economics, and increasing pressure from recreational diggers (Schink et al. 1984).]

High PSP toxin levels in oysters have required closures of commercial harvesting for one or two weeks during 6 years (1962, 1981, 1982, 1984, 1985, and 1986) and for one month in 1980. Mussel harvesting was closed for 3 weeks in the Santa Barbara area in 1985 (Price, D. pers.

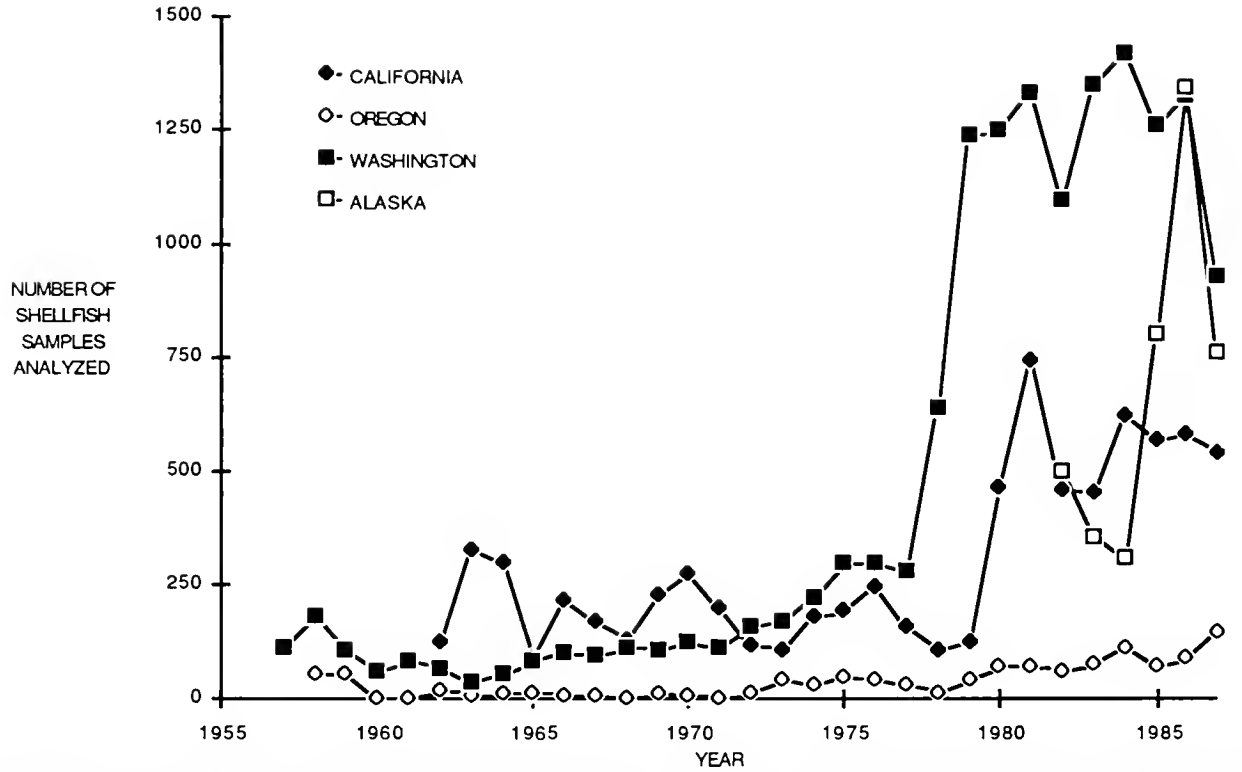

Figure 1. Number of shellfish samples analyzed for PSP toxins each year in California, Oregon, Washington, and Alaska (California data for 1962–1987—Price, D. pers. comm. Oregon data—Oregon State Health Division 1958–1987. Washington data—Washington Division of Health 1957–1987. Alaska data—Alaska Department of Environmental Conservation 1981–1987).

comm.). In most of these episodes, harvesting and income was slightly delayed, and no significant financial loss resulted from the closures. That was not the case in the 1980 outbreak when toxin levels were the highest ever recorded in California, with 16,000 μg in California mussels and 5500 μg in Pacific oysters (Sharpe 1981). The severe effects of the 1980 episode on the industry included losses due to the required destruction of harvested toxic oysters, the depressed market for all oysters (including those from areas without PSP closures) from July 1980–January 1981, a 50% summer mortality in 2-year-old oysters which were not harvested, and a disrupted flow of cash needed for maintenance and re-seeding. Total loss to the growers in California, Oregon, and Washington was estimated to be $630,000 (Conte 1984).

The sudden onset and rapid rise in toxin levels in California, apparently from the movement onshore of blooms originating offshore, pose a difficult challenge for the monitoring program—a program which safeguards the public health and, in so doing, protects the shellfish industry as well. This is true for aquaculture operations within bays, and even more so for those along the open coast and particularly at offshore installations. Because mussels increase in toxicity faster and to higher levels than most other species, their culture in such locations requires special attention to possible PSP hazards. The EPLHSB is exercising added caution in monitoring these additions to the industry.

OREGON

History of PSP Toxins in Shellfish

Several cases of shellfish poisoning were reported in the Coos Bay area (Figure 4) in the late 1920's and, in 1933, 20 illnesses and one death occurred on the Oregon coast (Halstead 1965). Only one PSP illness has occurred since then, in 1982 (Arnold pers. comm.). Monitoring on a semi-regular basis was begun in 1958, when high PSP levels were reported on the Pacific Ocean coast of Washington. Closure levels in razor clams (*Siliqua patua* Dixon) occurred in 1958; no toxicity was found in 1959; and monitoring was not resumed until 1962. A few samples (3–16) were analyzed each year until 1972 (no samples in 1968). Only 4 of the 102 samples taken from 1962–1972 had detectable toxin, the highest 31 μg. Prior to 1970 samples were primarily oysters and clams from commercial beds in bays. In 1970 the monitoring program shifted to California mussels from stations on the open coast. In 1973 a 3-week bloom affected the coast from the Columbia River to Coos Bay with toxin levels as high as 900 μg. Six harvesting closures have occurred in the 1980's: Two widely separated coastal areas near Tillamook Bay and Coos Bay had closures of one and two weeks in 1980 (with highest toxin values of 108 and 121 μg); the northern coast was closed for a week in 1981 (149 μg), for 3 weeks in 1984 (415 μg), and again briefly in 1987 (113 μg); and the coast near

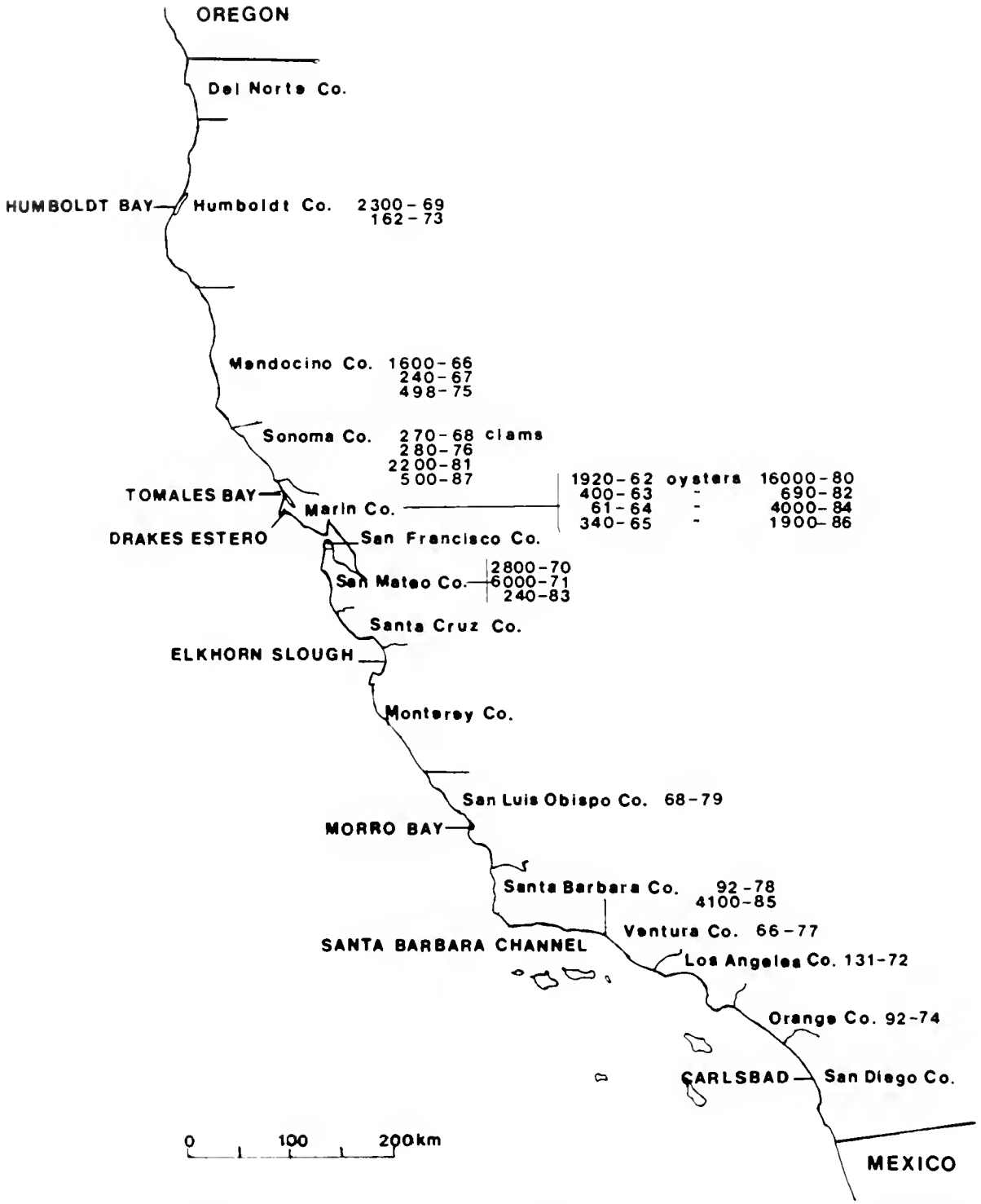

Figure 2. Coastline of California, with major shellfish production areas. The location of the highest reported toxin level during each year is noted: μg-year. All samples were mussels unless otherwise noted (Price, D. 1987).

Brookings was closed for 8 weeks in 1982 after a toxin level of 1675 μg was found in mussels, the highest level ever recorded in Oregon (Arnold 1986, pers. comm., Oregon State Health Division 1958–1987).

Although these records appear to indicate that the frequency of closures has increased in the 1980's, the data may be misleading. Because of the changes in the locations of monitoring stations and in species monitored, the frequencies of closure levels of toxin prior to and after 1970 are not comparable. These monitoring changes could be

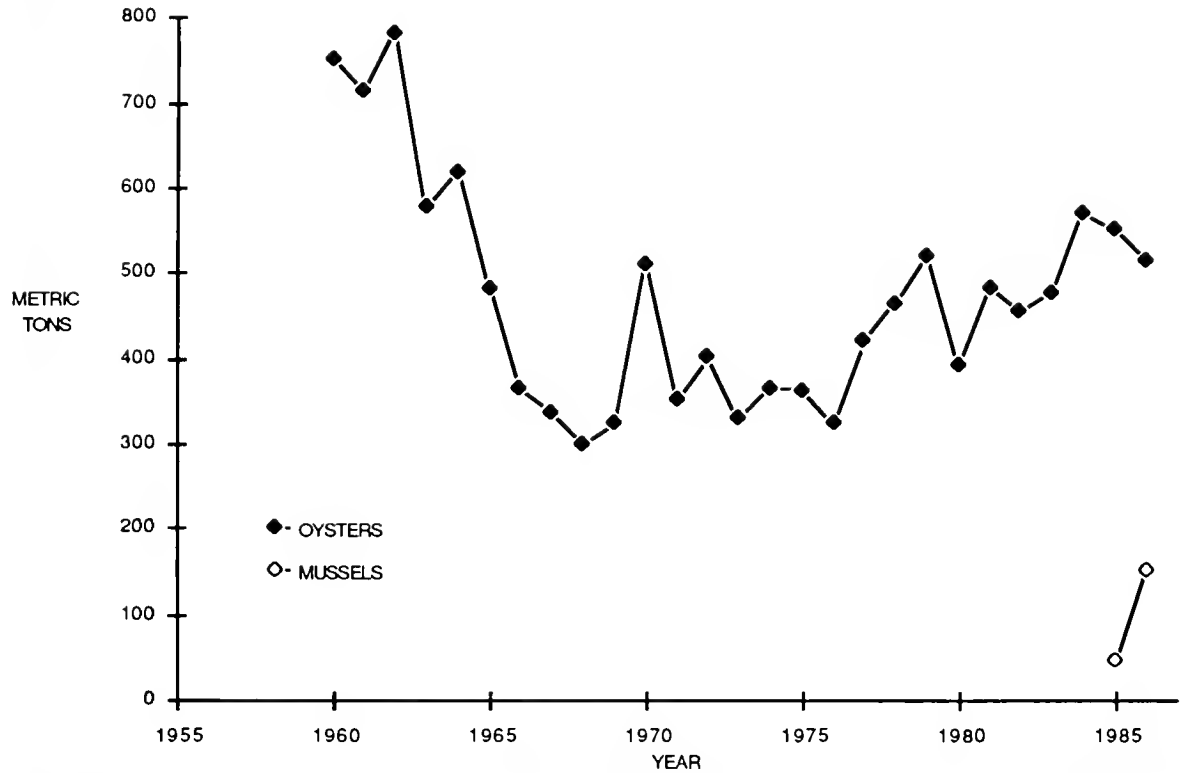

Figure 3. Production of oysters and bay mussels in California, 1960–1986, in metric tons. Shucked weight of oysters; shell weight of mussels (California Department of Fish and Game 1987).

expected to result in an increase in toxin values reported because mussels accumulate toxins more readily than oysters and because the blooms of the toxin-producing organism in Oregon appear to be initiated offshore rather than in bays. An earlier outbreak similar to that in 1973 might have been detected by the earlier monitoring program, but outbreaks similar to those of the 1980's would not have been detected. Further, comparison of closure frequency between the 1970's and 80's would be flawed because the coastal areas in which the outbreaks in 1981, 1984, and 1987 occurred were monitored during only three years in the 1970's. Episodes with toxin levels similar to those in 1981, 1984, and 1987 would not have caused symptoms and could have occurred during years without monitoring and passed undetected. Thus, the data available cannot be used to determine whether the apparent increase in frequencies of toxicity outbreaks in Oregon in the 1980's was, in fact, a real increase.

Prevention of PSP

The Oregon monitoring program has more than tripled since 1980 and in 1988 covers the 500 km coastline with 17 stations (Figure 4). From April to October weekly samples are collected, California mussels from the open coastal stations and Pacific oysters from the bay stations. During November through March commercially active sites will be monitored monthly (Phelps pers. comm.). Other species are monitored as circumstances require. The State Health Division monitors commercial shellfish operations, and the Department of Fish and Wildlife monitors areas used for recreational harvesting. When closures are required, the Health Division issues public service announcements which are followed by news media coverage (Arnold pers. comm.).

For many years the program was hampered by inadequate funding, partially because the occurrence of only two closures in the first 22 years of the program led many to assume that PSP did not pose a significant risk to public health or the shellfish industry. The 1988 expansion from 8 to 17 regular sampling stations has greatly improved the coverage of the monitoring program.

Shellfish Industry and PSP

The bivalve industry of Oregon underwent major changes in both the volume and the species produced during the decade from 1976 to 1986, as shown in Figure 5. The Pacific oyster, the most important aquaculture species, is produced primarily in Tillamook Bay, Yaquina Bay, and Coos Bay. During the decade production of this species underwent sharp fluctuations but generally increased, nearly doubling the volume produced (Oregon Department of Agriculture 1987). As in California, small amounts of European and eastern oysters have been produced in recent years. In contrast to the increase in oyster

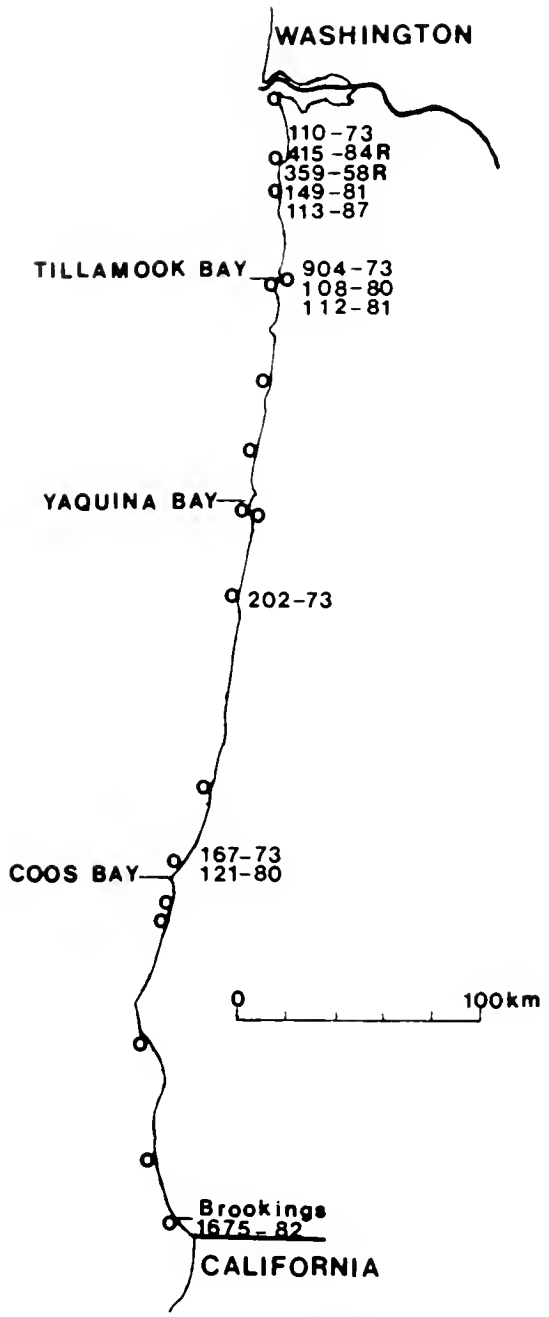

Figure 4. Coastline of Oregon, with major shellfish production areas and regular PSP monitoring stations (○). The locations of occurrences of toxin levels exceeding 80 μg/100 g shellfish meat are noted: μg-year. All samples were California mussels unless designated R for razor clams (Oregon State Health Division 1968–1987).

production, the harvest of razor clams declined to very low levels in the mid-1980's (with the exception of one high production year in 1985). The reason for the decline is not known; it appears to be unrelated to the infectious organism found in razor clams in Washington (Demory pers. comm.). Hardshell clam production, in total, has fluctuated sharply as major changes in the production of the several species have occurred. Gaper clams (*Schizothaerus capax* Gould), which accounted for nearly 100% of the hardshell harvest in 1976, comprised only 20% of the total in 1986. This decline is attributed to reduced recruitment and an annual 7-month all-species closure of Coos Bay, the main area of gaper clam production, because of bacterial contaminations during the rainy season. Between 1976 and 1986 production of cockles (*Clinocardium nuttalli* Conrad) and littlneck clams (*Protothaca staminea* Conrad) increased 100- and 60-fold to 39 and 33%, respectively, of the total hardshell production in 1986. The commercial harvesting of wild California mussels, insignificant prior to 1979, now equals that of any of the clam species. Far surpassing the production of bivalves in embayments and along the shoreline was the harvesting of natural beds of weathervane scallops (*Pecten caurinus* Gould) by offshore dredging. From 1979–1986 the harvest fluctuated widely with production in the peak years, 1981, 1983 and 1984, of 7.7, 1.2 and 1.5 thousand MT, respectively (Oregon Department of Fish and Wildlife 1976–1986).

When PSP toxin levels exceed 80 μg, the harvesting closure applies to all of the above species on the affected portion of the coastline. Closure levels of toxin in razor clams have been reported only twice since PSP monitoring began, in 1958 and 1984. Oyster and clam harvesting has been closed for short periods in Tillamook Bay five times and in Coos Bay twice since 1973. Toxin levels in weathervane scallops were below 80 μg in the years tested. These PSP harvesting closures have caused delays of harvesting but have not resulted in financial losses to the bivalve producers such as those experienced by California oyster growers in 1980.

WASHINGTON

History of PSP Toxins in Shellfish

In 1942 three persons died after eating clams and mussels from Juan de Fuca Strait, and high levels of toxicity occurred in razor clams on the open coast near Willapa Bay (Figure 6). The Department of Health (now the Department of Social and Health Services [DSHS]) imposed a harvesting closure for all bivalve species except razor clams from Dungeness Spit to the Columbia River from April 1–October 31. This closure regulation has been reissued every year since 1942. (Razor clams are exempt because they concentrate the toxins in the digestive gland which is removed before eating or processing.)

After a severe PSP outbreak in British Columbia in October 1957, a routine monitoring program, primarily for commercial shellfish, was initiated in waters north and west of Admiralty Inlet and in Willapa Bay and Grays Harbor. In the following years closure of levels of toxins were found frequently in shellfish in bays along Juan de Fuca Strait and rarely in the bays on the ocean coast. Between 1958 and 1971 monitoring shellfish areas used for sports harvesting was infrequent. After several years of irregular monitoring, closure levels of toxins were found for

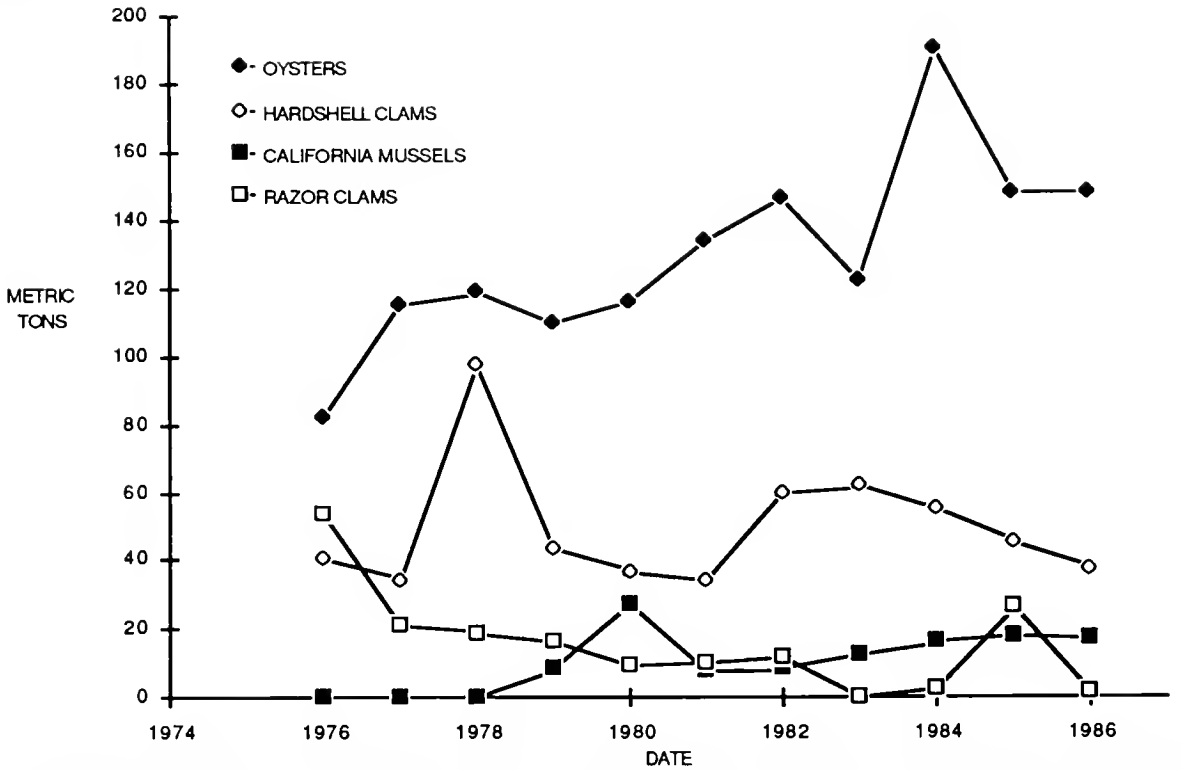

Figure 5. Production of bivalves in Oregon, 1976–1986, in metric tons. Shucked weight of oysters produced on state lands, estimated as 3.95 kg/gallon (Oregon Department of Agriculture 1987). Shell weight of other species (Oregon Department of Fish and Wildlife 1976–1986).

the first time at heavily-used clamming beaches in the San Juan Islands in 1971 and in the Bellingham area in 1973. Routine biweekly monitoring was initiated in those areas. In 1974 shellfish from a Samish Bay commerical operation, which had been monitored regularly since 1958, had toxin levels which required closure for the first time. Since then closure levels have occurred in that bay for short periods every year but one.

Prior to 1978 no PSP illnesses had been reported from consuming of shellfish harvested in Puget Sound, which consists of four major basins east or south of Admiralty Inlet (Hood Canal and Whidbey, Central and Southern Basins). Routine PSP monitoring in those waters was conducted at only one station at the north end of the Central Basin, beginning in 1975, and at a mussel farm in the Whidbey Basin, starting in 1977. Prior to September 1978 low levels of toxin (highest, 64 μg) were detected in one-fourth of the samples at the Central Basin station and no toxin was reported in the Whidbey Basin. Widespread toxicity occurred in September 1978, beginning in the Whidbey Basin, where toxin levels in bay mussels were as high as 30,000 μg. Ten persons reported PSP symptoms after consuming of sports-harvested bay mussels and pink scallops (*Chlamys hastata* Sowerby). No deaths occurred (Washington Office of Public Health Laboratories and Epidemiology 1978). Toxic shellfish were found as far south as Des Moines in 1978 and at the northern end of the Southern Basin in 1979 (Nishitani and Chew 1982). A survey of the Southern Basin in 1981 found either motile cells or cysts of *Gonyaulax catenella* or low levels of toxin in shellfish in all sections of that basin (Nishitani unpublished data). The first closure levels of toxins in the Southern Basin occurred in October 1988, when levels as high as 2000 μg were found in oysters. Toxin levels requiring harvesting closure have never been reported in Hood Canal (Washington Division of Health 1957–1987).

It is not possible to determine whether the occurrence of low toxin levels in Hood Canal and the Southern Basin in the decade after the 1978 episode represents an actual spread of toxicity into those waters following that outbreak in other parts of Puget Sound. Similar low levels could have occurred prior to 1978 and gone undetected because those two areas were not monitored regularly and such low toxin levels, had they occurred, would not have caused illnesses which would have been reported. However, monitoring data provide direct evidence that a marked increase in toxin levels occurred in the Bellingham area in 1976 and in both the San Juan Islands and the northern Central Basin in 1978. Indirect evidence of the increased toxicity throughout the Whidbey Basin and Central Basin is provided by repeated occurrences since 1978 of toxin levels exceeding 1000 μg, which could be expected to cause PSP symptoms (Figure 6). The fact that there were no earlier reports of PSP illnesses from consumption of shellfish from

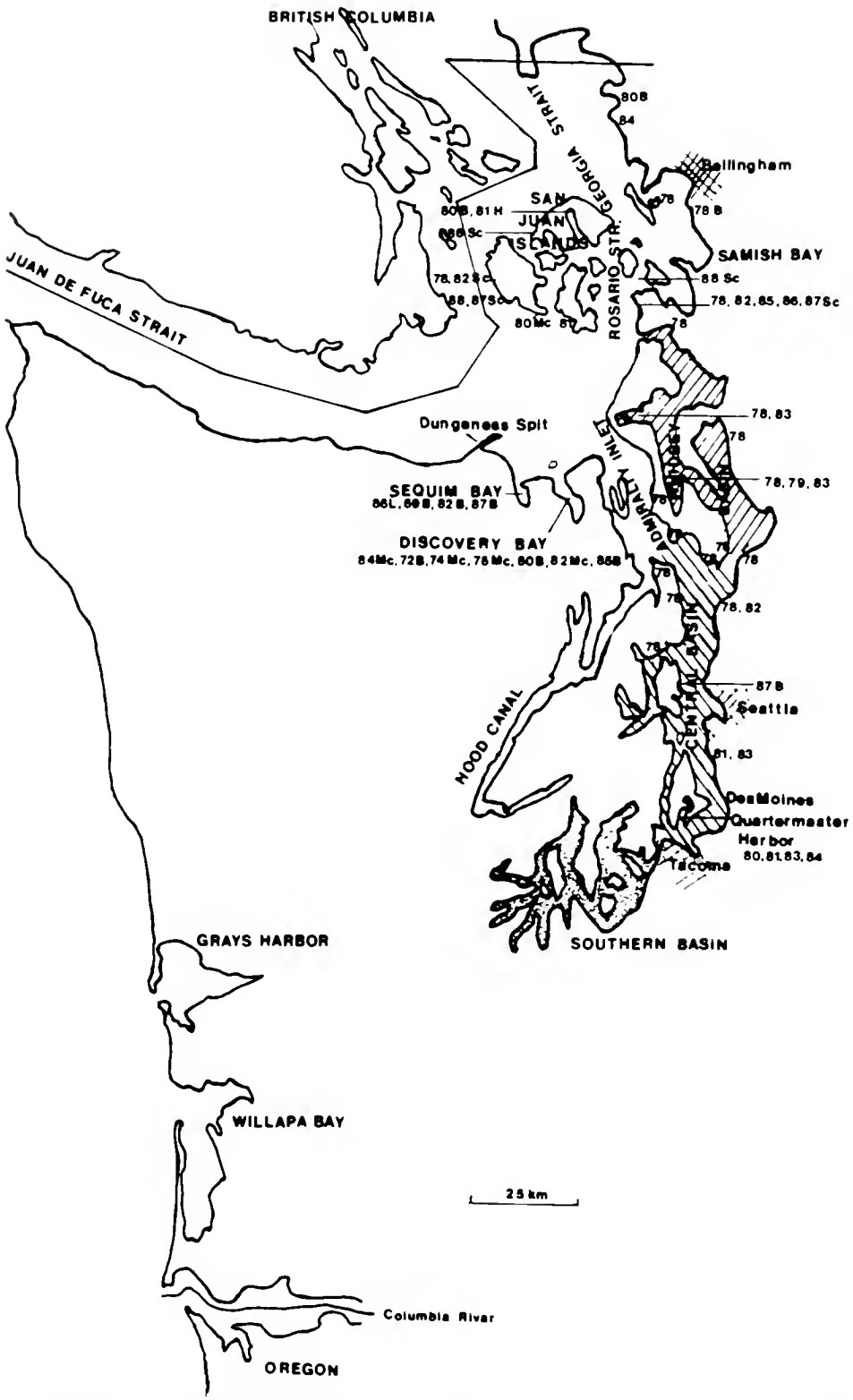

Figure 6. Coastline of Washington, with major bivalve production areas. Years of occurrences of toxin concentration exceeding 1000 μg toxin/100 g shellfish meat are noted. Species tested were bay mussels unless symbol indicates other species: B, butter clam; Mc, California mussel; L, littleneck clam; H, horse clam (*Schizothaerus capax* Gould); Sc, pink scallop. ●, occurrence of toxins exceeding 20,000 μg/100 g shellfish meat in 1978. Because of the annual closure from April 1–October 31, shellfish along the coastline from Dungeness Spit to the Columbia River are not monitored for PSP regularly, except in Grays Harbor and Willapa Bay.

those basins (where heavy recreational harvesting occurs) suggests that similar concentrations of toxins had not occurred there previously.

As in California and Oregon, the occurrence of toxic shellfish along the ocean coast and in coastal bays appears to have been caused by blooms which originated in the ocean, not in bays. Four of the five such episodes since 1942 have occurred during, or at the cessation of, strong El Nino/Southern Oscillation events (Erickson and Nishitani 1985). In contrast, in inland waters blooms originate *in situ*, and toxicity may be widespread or highly localized. In Quartermaster Harbor, a study area in the Central Basin, onset of early summer blooms and mussel toxicity has been shown to be dependent on development of a surface water layer with favorable temperatures (14°C) to a depth of several meters. These physical conditions developed faster and closure levels of toxicity in mussels occurred earlier within the bay than in adjacent channels more subject to wind-driven turbulence (Nishitani and Chew 1984). Other factors controlling onset and duration of blooms were shown to be limiting concentrations of either nitrogen or phosphorus and parasitism by the dinoflagellate *Amoebophrya ceratii* (Koeppen) Cachon. [The possibility of using this parasite as a biological control agent was investigated and rejected because it also attacks several other species of dinoflagellates which at times are the dominant phytoplankters in Washington waters (Nishitani et al. 1984, Nishitani et al. 1985)].

While toxicity in mussels closely reflects the seasonality of *G. catenella* blooms, toxicity in butter clams (*Saxidomus giganteus* Deshayes) and pink scallops does not. These two species have maintained toxin levels exceeding 80 μg year around in certain areas (Washington Division of Health, 1957–1987). It is not known whether these elevated toxin levels during winter and spring are due to retention of toxin from the previous summer or to ingestion of toxic cysts.

Prevention of PSP

Preventing PSP in Washington is a difficult task complicated by the extensive (>2700 km) shoreline, portions of which are highly convoluted and provide physical settings for very localized blooms of *G. catenella,* by the various patterns of uptake and retention of toxins in different shellfish species commonly harvested, and by governmental delegation of the responsibilities for PSP prevention in part to the State and in part to the separate health departments of the 14 counties with marine shorelines.

Monitoring for PSP toxins and setting closures for commercial harvesting is the responsibility of the Office of Environmental Health (OEH) in the DSHS. This agency also advises the county health departments which are responsible for monitoring and regulating PSP closures of recreational harvesting. The monitoring schedule for commercial harvesting varies with conditions. Biweekly sampling of commercial species is conducted in most areas during harvesting periods. In Hood Canal where closure levels have never occurred and in the Southern Basin where the first harvesting closure occurred in October 1988, OEH sampled only mussels on a monthly basis through 1987. Monitoring of commercial species in both areas was initiated in the spring of 1988. In several areas when toxin levels approach 80 μg, lot sampling after harvesting and before marketing may be required (Cox pers. comm.).

The OEH requests that counties collect samples biweekly from April through October at recreational sites along Juan de Fuca Strait east of Dungeness Spit, in Whidbey Basin and Central Basin, and in the northern inland waters. Intermittent winter sampling is conducted in those areas also. The 550 km shoreline subject to the seasonal closure (Dungeness Spit to the Columbia River) is sampled infrequently. The species monitored vary, bay mussels in the Southern Basin and near Seattle, littleneck or butter clams elsewhere. The types of closures vary widely with circumstances. Some closures are applied to all species over large areas which are impractical to monitor regularly, leaving open only those sites which have been tested and shown to have low levels of toxin. In other areas closures may apply to specific bays and be restricted to one or a few species. Information about recreational harvesting closures is disseminated by the news media and by a toll-free PSP hotline provided by OEH. Some beaches are posted with multilingual signs designed to protect and inform recent immigrants (Lilja pers. comm.).

The consequence of the increase in toxicity levels which occurred in the 1970's was a ten-fold increase in number of samples analyzed annually, to 1300 (Figure 1). Most of this increase in samples has stemmed from the need to provide protection for recreational harvesters, and only a small portion has resulted from new operations at several small shellfish farms. The result is that currently more samples are from recreational harvesting beaches than from commercial operations, a reverse of the situation in 1970.

The OEH views inadequate coverage of the shoreline (due to limited funding at both the state and county levels) and the lack of public compliance with closures as two continuing problems in preventing PSP. The non-compliance stems partially from lack of understanding of the potential severity of PSP and the degree of risk when eating shellfish from a closed area, and points to the need for more public education about PSP (Cox pers. comm.). To that end, the Washington Sea Grant Program published and widely distributed a general information pamphlet about PSP (Nitshitani and Chew 1982).

The success of the monitoring program can be measured by the level of public health protection provided and by the degree to which the shellfish industry is able to function around the PSP problem. Prior to the occurrence of 2 confirmed PSP cases during the 1988 episode, there had been no illnesses from shellfish produced in commercial operations since the monitoring program began in 1957. Despite

the large increase in the areas in which toxicity rises annually to levels which could cause illness or death, the only reported PSP illnesses from sports-harvested shellfish were the 10 cases from mussels and pink scallops at the beginning of the 1978 unexpected bloom in a 'safe' area, 3 cases from clams in 1979, and 3 from scallops in 1985 in areas where harvesting was closed. Harvesting by commercial producers has been kept open as much as possible, consistent with public health protection, by frequent sampling during closure periods, by lot sampling and by implementing harvesting closures by species rather than by area so that harvesting of those species with toxin levels less than 80 μg could continue.

Effects of PSP Toxins on the Shellfish Industry

As in California and Oregon, the bivalve industry in Washington has undergone marked changes since 1970, in terms of the size of the industry and the species produced (Figure 7) (Washington Department of Fisheries 1987, 1988). Despite the large expansion of the area affected by PSP toxins, these changes in the industry have been influenced relatively little by toxicity problems.

Oysters have historically dominated the Washington bivalve industry. The Pacific oyster is the major species, with the Olympia oyster (*Ostrea lurida* Carpenter) and the European oyster comprising less than 1% of the oyster production. Oysters are grown primarily in Willapa Bay and Grays Harbor, which together produce nearly 60% of the state total, and in the Southern Basin. Short-term closures for PSP toxins have occurred only once in Grays Harbor and twice in Willapa Bay since 1957. No PSP closures occurred in the Southern Basin prior to October 1988. Small oyster operations in the northern inland waters have had short-term closures for toxicity since 1974 and have infrequently experienced relatively small losses when harvested oysters had to be destroyed after testing high in PSP toxins. The extent and duration of the effect of the 1988 outbreak on the industry are unknown at present (one week after the outbreak.)

The razor clam industry on the Pacific coast beaches has had short-term closures for PSP toxins only four times since 1942. This fishery, which accounted for 7% of the total value of bivalves in 1970, has been drastically reduced by a large-scale mortality. An infectious organism, nuclear inclusion X (NIX), "can be strongly but presumptively linked" to the mortality (Elston et al. 1986).

Prior to the major outbreak of toxicity in 1978 harvesting closures had occurred intermittently in Sequim Bay and Discovery Bay, major bays for production of littleneck and butter clams. Production of both species declined during the 1978 episode. Since 1979 harvesting closures for butter clams, which retain the toxins for long periods, have extended year-round in those bays and have been intermittent in other bays. Closures for littlenecks have been less extensive. Closures and marketing problems have resulted in the virtual elimination of the butter clam industry,

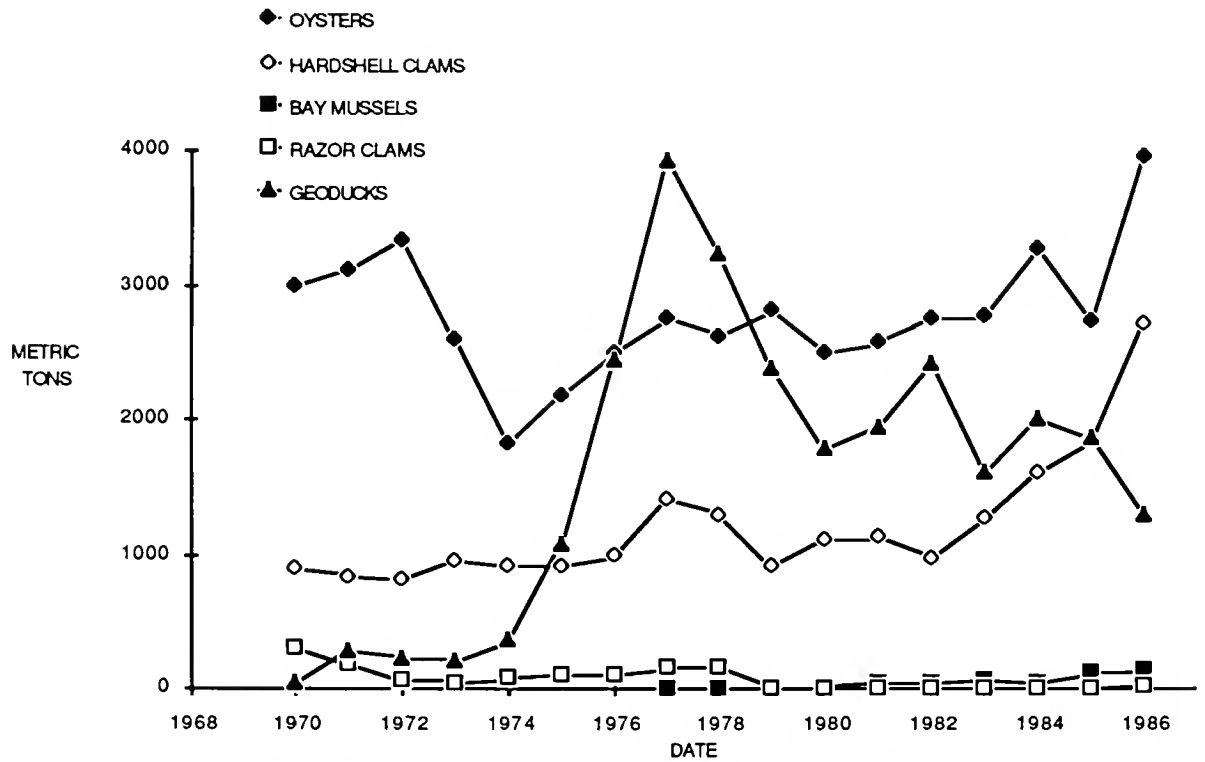

Figure 7. Bivalve production in Washington, 1970–1986, in metric tons. Shucked weight of oysters; shell weight of all other species (Washington Department of Fisheries 1985, 1986).

which contributed one-third of the total hardshell clams in 1970. Shellfish operations in those bays now harvest littlenecks exclusively, working around PSP closures which are spotty in distribution and of relatively short duration for this species. Closures cause inconvenience but have not caused major loss of production (Gunstone pers. comm.). Manilla clams (*Vernerupis japonica* Deshayes) are harvested mainly in the Southern Basin where PSP closures had not occurred prior to 1988. With a nearly 7-fold increase in production of this species and a marked rise in prices, the value of hardshell clams had risen from 6% of the total value of bivalves in 1970 to 27% in 1986.

Large-scale harvesting of geoducks (*Panope generosa* Gould) started in 1975, peaked in 1977, and in 1986 contributed 10% of the value of bivalves. PSP toxins have not affected this industry because the gut portion, the only part of the clam in which 80 μg toxin has been reported in Washington, is discarded before processing.

Bay mussels are cultured at several sites in Puget Sound, with first harvests in 1977. The new operations in the Whidbey Basin were closed for 6 months following the 1978 outbreak. Some growers in that area have had one or a few short-term PSP closures since then; others, in a bay with annual recurrences of closure levels of toxicity, have relocated in the Southern Basin.

In the 1980's small diving operations have conducted exploratory fisheries for pink scallops in Admiralty Inlet and in the San Juan Islands-Rosario Strait area. Scallops are known to be widespread and very abundant, but the potential value of the resource has not yet been assessed (Cox pers. comm.). Production in 1986 was 20 MT. It remains questionable whether a successful scallop industry can be established because this species, which is eaten whole, has been found to have toxin levels exceeding 80 μg in more than half the samples in summer and fall, and in at least one-tenth of the samples during winter and spring (Washington Division of Health 1957–1987). In the absence of Interstate Shellfish Sanitation Conference (ISSC) regulations covering scallops, OEH has entered into agreements with the scallopers regarding toxin levels in scallops being marketed. However, these agreements are nonbinding, and the potential for toxic pink scallops entering the market cannot be ruled out (Lilja pers. comm.).

ALASKA

History of PSP Toxins in Shellfish

Since the first episode of mussel poisoning in Alaska when 100 men of the Baranoff expedition died in Peril Strait (Figure 8), 174 additional PSP illnesses have been

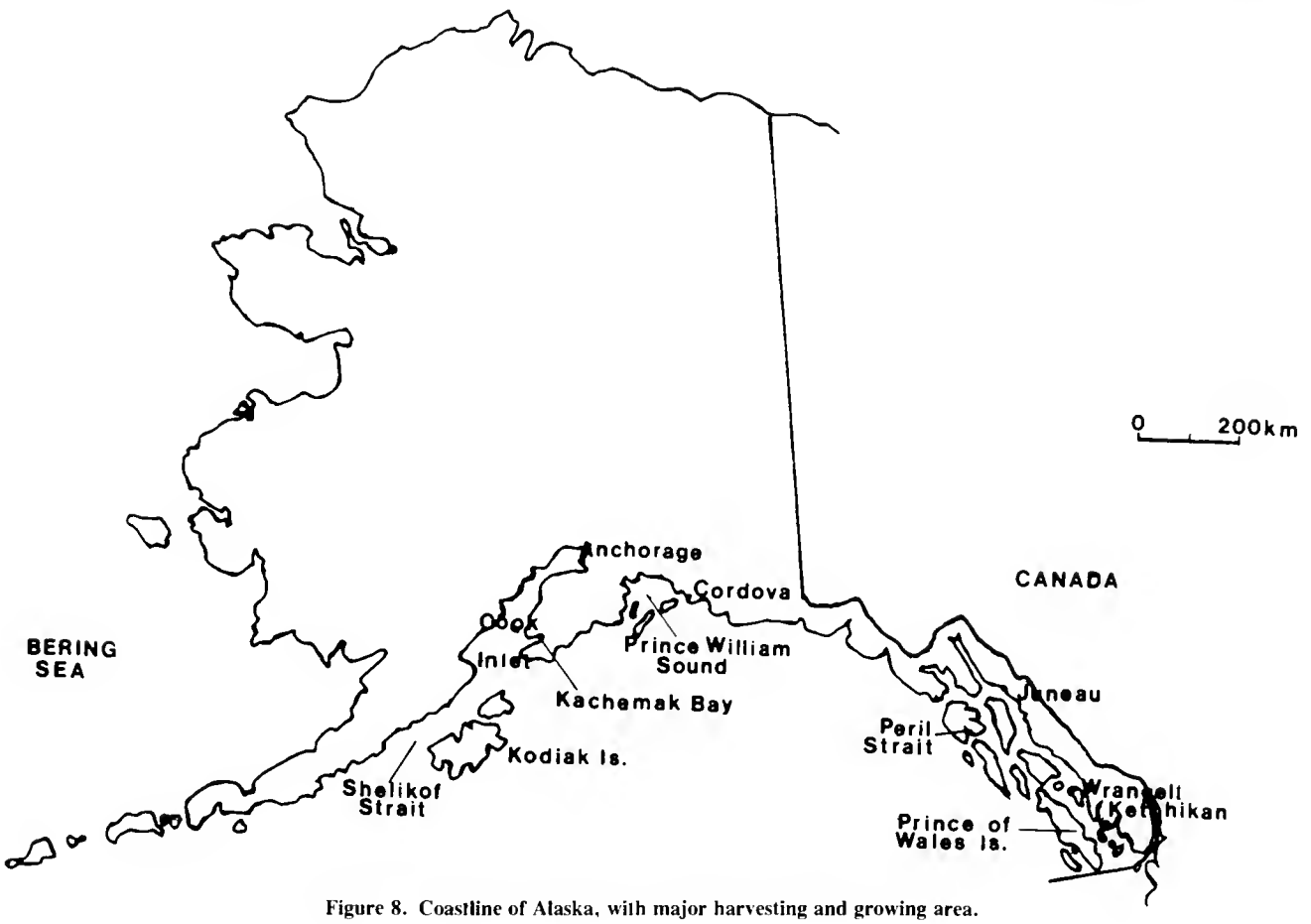

Figure 8. Coastline of Alaska, with major harvesting and growing area.

recorded (Table 1). Despite increased awareness of the hazards of shellfish toxicity and warnings by the Alaska Department of Health and Social Services, the frequency of PSP episodes among recreational harvesters appears to be increasing. There were outbreaks in only one or two years during each decade from 1930–1969, in 5 years during the 1970's, and in each year from 1980–1987 (Table 1). From 1976–1987, 40 separate outbreaks of PSP illnesses occurred (Middaugh 1987b). Whether the apparent increase in frequency reflects an actual increase in occurrences of high levels of toxicity in shellfish or is a function of human factors such as increased recognition, improved reporting or the rapid increase in the population is unknown. Lack of awareness of the risks of PSP among new residents and tourists may contribute to the increase in PSP cases in recent years (Middaugh pers. comm.).

Because the State of Alaska does not attempt a surveillance program of the more than 5000 km of shoreline, shellfish toxicity data are available primarily for those areas which either support commercial shellfish operations currently or have been investigated as potential commercial harvesting sites. After the butter clam industry was closed in the late 1940's because of high toxicity on the beaches traditionally harvested, extensive sampling was conducted in search of areas with butter clams with low toxin levels. This survey indicated that toxin levels were generally lower in shellfish from the outer coast of Prince Wales and Baranof Islands than in bivalves from the inside waters. It was noted that clams from exposed locations near mouths of bays were more toxic than samples taken near the heads. In the Ketchikan area butter clams were toxic during the entire year (Hayes 1965). In a 1985–87 cooperative study by the Department of Fish and Game and Department of Environmental Conservation, similar year-round toxicity in butter clams was found at several beaches in the Juneau area. In that study toxicity in bay mussels, littlenecks, and cockles was seasonal, highest in June and July. Between 1982 and 1987 only 1% of all razor clam samples from the approved harvesting areas (Cook Inlet, the Cordova area, and Shelikof Strait) had toxin above detectable levels, none above 80 μg. In 1975 during an extensive bloom 3 and 5% of razor clam samples in two approved areas had levels exceeding 80 μg and harvesting was closed. Hardshell clams, sampled extensively in the approved harvest area of Kachemak Bay in 1985–87, had no toxin level above 80 μg (Alaska Department of Environmental Conservation 1981–1987). However, these records of low or no toxicity from areas generally considered 'safe' enough to be approved for harvesting cannot be considered indicative of toxin levels in other areas. In 1987 bay mussels in the Kodiak area, sampled after two cases of PSP illness, had >5000 μg toxin (Middaugh 1987b).

Prevention of PSP

There is no closed season for recreational harvesting as in California and in portions of the Washington coast. All Alaskan beaches are considered at risk at all times. (Outbreaks of PSP have been documented in January, February, March, April, May, June, July, August and October.) Warning signs are posted on some beaches, in southeast Alaska cities and in Alaskan ferries. When high levels of toxins in shellfish are found or an outbreak of PSP reported, news releases with warnings and information stimulate extensive publicity. In addition, the Department of Health and Social Services worked with the Department of Fish and Game to include warnings about the dangers of PSP in the Fish and Game regulations that are distributed at the time an individual purchases a fishing license (which is required for recreational clamming) (Middaugh pers. comm.).

Commercial harvesting is restricted to 30 sites which have been approved for harvest and are subject to a lot control and site monitoring system (Stott pers. comm.). The primary purpose of the monitoring program is to test samples of commercially harvested shellfish. The Division of Environmental Health in the Department of Environmental Conservation (DEC) administers the program and conducts the assays. Samples are collected by the Department of Fish and Game, DEC, the Division of Public Health and shellfish harvesters. The current monitoring procedure for commercial harvesting involves an annual monitoring of areas approved for commercial production. For all species other than razor clams the annual monitoring is followed by sampling of each lot harvested prior to marketing (Barrett pers. comm.). The number of samples tested annually is increasing as new aquaculture operations start producing, with nearly 800 samples in 1987, following a high of 1400 samples during a special study in 1986 (Figure 1).

Effects of PSP Toxins on the Shellfish Industry

In the first half of this century the bivalve industry in Alaska, based on razor clams in Cook Inlet and the Cordova area and butter clams in southeast Alaska, peaked at more than 2000 MT and became more or less stabilized at 700–900 MT annually (Orth et al. 1975). The butter clam operations were essentially destroyed in 1946, when new federal regulations regarding PSP toxins took effect, because of the year-round presence of toxins in that species (McFarren et al. 1960). A fishery for cockles continued and increased, peaking at 591 MT in 1960. It ended in 1962, in part because of PSP restrictions (Nosho 1972).

Because razor clams concentrate the toxins in the digestive gland which is discarded prior to consuming or processing, the razor clam industry was able to continue, harvesting for both the bait and human consumption markets. However, in 1954 the US Public Health Service withdrew Alaska from the National Shellfish Sanitation Program (NSSP) because of its apparent inability to meet the Program's requirements for assurance of safe products. That action precluded inter-state shipments of fresh and frozen

clams for human consumption. (A further setback to the industry was experienced when the 1964 earthquake destroyed 43% of the razor clam habitat in the Cordova area by raising the beaches and made razor clams in Cook Inlet less accessible by lowering beaches. Habitat recovery has been very slow.) In 1970 the Department of Health and Welfare (later changed to the Department of Health and Social Services) restricted the harvesting of razor clams to three approved beaches, near Cordova and in Cook Inlet and Sheilikof Strait. It maintained a surveillance program based on biweekly sampling at key stations at those 3 beaches until 1977. Samples were analyzed by the Public Health Laboratories as part of the PSP testing program it had initiated in 1960. In 1977 responsibility for PSP monitoring was transferred to the Department of Environmental Conservation (Middaugh pers. comm., Stott pers. comm.). Procedures adopted in 1973 for on-the-beach dyeing of razor clams for bait have permitted continued bait harvesting at other beaches. Alaska regained access to the inter-state human-consumption market in 1975 when it was re-admitted to the NSSP (Orth, et al. 1975). Production figures (Figure 9) indicate the recovery of the razor clam industry.

The offshore fishery for weathervane scallops, begun in 1968, has had large fluctuations in production, with an average of 260 MT from 1980–86. Very limited testing (4 samples) has shown PSP toxin levels in the adductor muscle to be below closure level when other parts of the animals had toxin levels up to 12,000 μg (Alaska Department of Environmental Conservation 1981–1987).

Both governmental agencies and private enterprise have been involved in efforts to increase the utilization of both the vast native bivalve resources and the aquaculture potential of the numerous protected embayments. In 1982 the lot sampling system for PSP analysis was initiated, permitting the harvest of species other than razor clams. Exploratory surveys by DEC, Department of Fish and Game, and a private company have been conducted to determine the feasibility of geoduck harvesting. Of several hundred animals tested, from Prince of Wales Island and the Ketchikan area, only one animal had detectable toxin (35 μg) in its siphon; no toxin was detected in the mantles; and the viscera of 21 and 8% of the animals in the two areas had >80 μg toxin, up to 255 μg. Because viscera are discarded before processing, PSP analyses of geoducks to be processed are restricted to siphons and mantles. In the case of geoducks to be shipped live, only the viscera are analyzed. Commercial production of geoducks rose from 0.1 MT in 1983 to 59.5 MT in 1986 (Figure 9). Other private enterprises have helped to diversify the shellfish industry: A company harvesting wild hardshell clams (mostly littlenecks) and a mussel grow-out operation, both in Kachemak Bay, and oyster farms near Wrangell and Prince of Wales Island (Ostasz pers. comm.). The oyster operations are still small with less than 1 MT produced in 1984 and no commercial harvest reported thereafter. Both oyster operations have had short periods with toxicity exceeding 80 μg. In 1985, 0.2 MT of surf clams (*Spisula polynema* Dall) were harvested; no subsequent harvest has been reported (Alaska Department of Fish and Game 1976–1987).

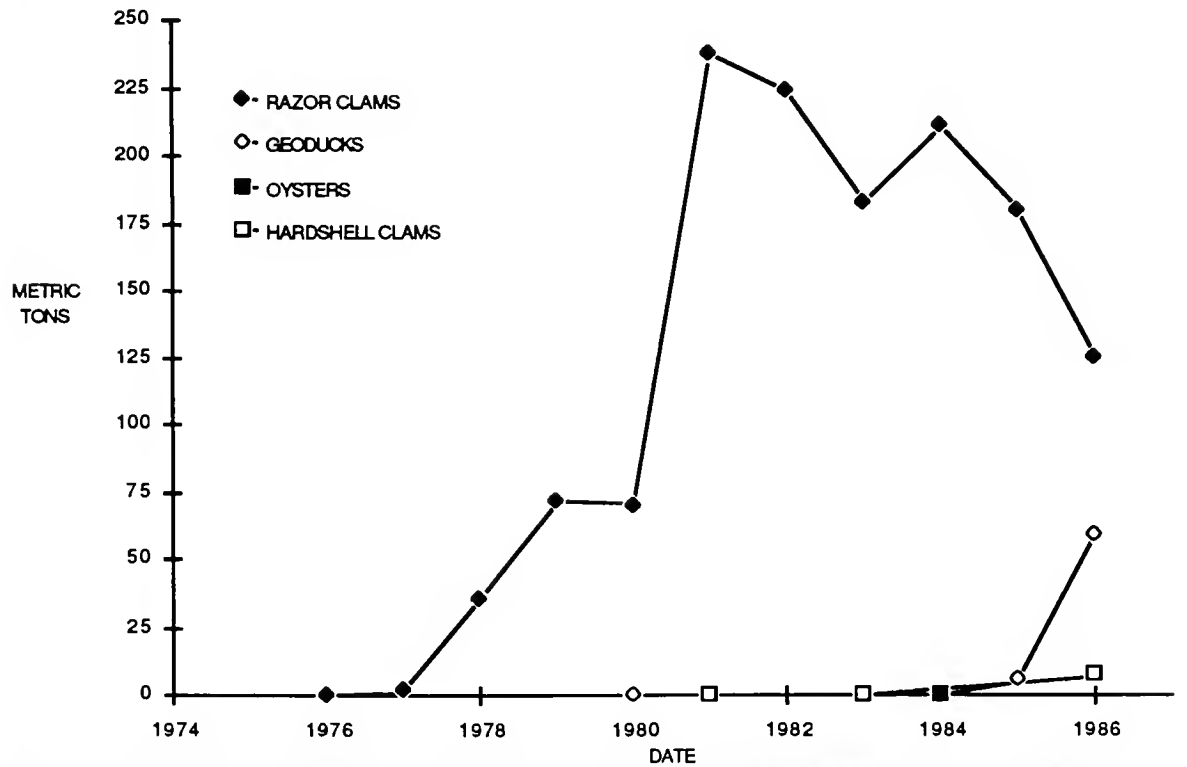

Figure 9. Bivalvle production in Alaska, 1976–1986, in metric tons, shell weight (Alaska Department of Fish and Game 1976–1987).

The level of interest in expanding both the aquaculture operations and the harvesting of wild stock is indicated by the fact that 60 applications for certification of harvesting areas are being processed by the Division of Environmental Health (Ostasz pers. comm.). The potential sustainable yield of wild bivalve shellfish in Alaskan waters has been estimated to be in excess of 22,000 MT (Orth et al. 1975). The Bering Sea resource alone, comprised of the surf clam and the tellin (*Tellina lutea* Wood), is estimated to have an annual sustainable yield worth $12–20 million (Lutz and Incze 1979). The extent to which PSP toxins will limit the harvesting of these vast resources remains unknown.

CONCLUSIONS

Records of PSP monitoring programs and of PSP illnesses indicate that the threat of outbreaks of PSP toxins in shellfish exists along the Pacific coast of North America from Alaska to California. To date the frequency and intensity of episodes has been less in Oregon than in areas north or south of that state. In all four continental Pacific states there has been an apparent increase in frequency of episodes of either PSP illnesses or high PSP toxin levels in shellfish, beginning in the mid-1970's in Alaska and Washington, and in the early 1980's in Oregon and California.

The repeated occurrences of toxicity outbreaks at unexpected times or in unexpected places (Washington 1978, California 1980, 1984, 1985, Oregon 1982) underscores our lack of ability to predict major blooms and emphasizes the essential role of the monitoring programs in protecting both the public health and the shellfish industry. The 1980 episode demonstrated the dependence of the bivalve industries in each of the Pacific states on the monitoring and public education programs of each of the other states.

Despite the apparent increase of occurrences of high PSP toxin concentrations in shellfish, aquaculture and the harvest of wild bivalves have increased in all four states in the last decade. This expansion of areas and diversification of species has necessitated the expansion of the monitoring program of each of the states. Lot sampling procedures adopted in Alaska and Washington extend the harvesting periods and areas in waters in which closure levels of PSP occur frequently. Even with this procedure (which requires a considerable additional commitment by the state for sample analyses), it is probable that continued presence of closure concentrations of PSP toxins will preclude the utilization of large portions of the Alaskan bivalve resources and, on a much smaller scale, preclude the commercial harvesting of certain species in Washington.

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A SHIFT IN PHOTOSYNTHETIC PICOPLANKTON COMPOSITION AND ITS EFFECT ON BIVALVE MOLLUSC NUTRITION: THE 1985 "BROWN TIDE" IN NARRAGANSETT BAY, RHODE ISLAND

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ABSTRACT An unprecedented algal bloom occurred as a "brown tide" in Narragansett Bay, Rhode Island, during the summer of 1985. Water samples analyzed by epifluorescence and transmission electron microscopy revealed unusual changes in the composition of the picoplankton. Total bacterial numbers during peak bloom conditions were 10^7 cells ml^{-1} or 10-fold greater than usual for the summer coastal picoplankton. Among the photosynthetic forms, a 1.5–2.0 μm diameter chrysophycean alga was observed at a concentration of about 10^6 cells ml^{-1} and 95% of the total phytoplankton by numerical abundance. Further, the concentration of photosynthetic cyanobacteria (e.g., *Synechococcus*) were reduced 10-fold from typical densities of 5×10^5 cells ml^{-1}. Experiments using mussels (*Mytilus edulis*) demonstrated reduced feeding on bloom algae, whereas optimal clearance rates were obtained with a similarly-sized strain of *Synechococcus* fed at comparable densities. These observations of normal and inhibited feeding on different components of the picoplankton suggest the species composition of the picoplankton may affect the nutrition and hence growth of this bivalve mollusc.

KEY WORDS: Picoplankton composition, brown tide, mussel, *Mytilus edulis*, bivalve nutrition, Narragansett Bay

INTRODUCTION

The availability and composition of suspended particulates are both widely recognized as critical environmental parameters that govern the growth of marine bivalve molluscs. The bulk of information concerning the nutritional requirements of bivalves has arisen from an interest in cultivation (see Winter 1978 for review). The effects of a variable food supply and the quality of food on the ecology of natural bivalve populations recently has received considerable attention (Widdows et al. 1979, Kiorboe et al. 1980, 1981, Bricelj and Malouf 1984, Berg and Newell 1986). In estuarine and offshore waters, a significant fraction of the biomass and primary productivity may be attributed to photosynthetic micro-organisms 0.2–2 μm in diameter (Li et al. 1983, Platt et al. 1983, Davis et al. 1985). These micro-organisms have been termed picoplankton (Sieburth et al. 1978, Stockner and Antia 1986).

Given that many bivalves can retain particles as small as 0.5 μm (Mohlenberg and Riisgard 1978), the contribution of picoplankton to the nutritional requirements of the animal may be significant when larger food particles are not available (Wright et al. 1982, Lucas et al. 1987). However, the gross morphological characteristics of picoplankton observed by light microscopy are insufficient for cell differentiation, thus the effect of picoplanktonic composition on bivalve nutrition has received little attention. What little is known of their detailed morphology and taxonomy in natural populations has been obtained by transmission electron microscopy of thin sections (Johnson and Sieburth 1982).

In this note, we describe the shift in the photosynthetic picoplankton from a cyanobacterial to an algal-dominated composition during a "brown tide" in Narragansett Bay, Rhode Island during the summer of 1985, and its effect on particle removal by the blue mussel, *Mytilus edulis*. A more complete characterization of the morphology and ecology of the "brown tide" organism, *Aureococcus anophagefferens* (formerly *Pardococcus anorexus* nom. prov., Sieburth et al. 1986) has been described elsewhere (Sieburth et al. 1988). The data presented here will demonstrate

importance of picoplanktonic composition on the nutrition of this bivalve mollusc and possibly other species as well.

MATERIALS AND METHODS

Picoplankton Characterization

Surface seawater samples were collected from the pier at the University of Rhode Island's Graduate School of Oceanography, Narragansett, RI during summers prior to 1985, during peak bloom conditions (2 July 1985) and during late bloom conditions (29 July 1985). Samples were fixed immediately with 1% gluteraldehyde. Epifluorescence microscopy of DAPI-stained particles on 0.2 μm Nucleopore filters was used to determine total bacterial numbers (Sieracki et al. 1985). Visual counts on unstained preparations by epifluorescence microscopy were used to enumerate the 1–2 μm diameter cyanobacteria (yellow autofluorescing) and unicellular algae (red autofluorescing). Sub-samples were processed for transmission electron microscopy (TEM) of thin sections by the procedures of Johnson and Sieburth (1982).

Physiological Measurement

Mussels (4.5–5.5 cm length, 0.73 ± 0.25 g dry tissue weight) were collected from a sub-tidal population in lower Narragansett Bay (71°24.0′N by 41°29.4′W). Animals were placed individually within grazing chambers and fed either a phycoerytherin-containing strain of *Synechococcus* isolated from the bloom (and cultured on PES media, McLachlan, 1973) or bloom algae (dominated by *Aureococcus*, see results) within Narragansett Bay water collected during the height of the bloom.

Sargasso Sea water diluted to Bay salinity (30 ppt.) with deionized water was used as a source of seawater that was free of bloom exudates. Desired test concentrations of bloom algae were achieved by dilution. In order to conserve diluting water, the clearance of bloom algae was estimated using the method of Coughlan (1969):

$$CR = M/(n \times t) \log_e (\text{Conc. } t_1/\text{Conc. } t_2)$$

where CR = clearance rate (ml min^{-1}); M = volume of suspension within the grazing chamber (ml); Conc. t_1 = initial concentration at time t_1; Conc. t_2 = final concentration at a subsequent time t_2; and n = number of individuals (i.e., 1 in this case).

Feeding experiments with *Synechococcus* were conducted during a non-picoalgal bloom period, but at similar conditions of temperature (20°C) and salinity (30 ppt.). Narragansett Bay seawater filtered at 1.0 μm was used to dilute *Synechococcus* cultures to desired test concentrations. The clearance rate of *Synechococcus* by mussels was estimated using the method of Hildreth and Crisp (1976):

$$CR = (C_1 - C_2)/C_2 \times F$$

where C_1 and C_2 are the concentration of particulates entering and leaving the grazing chamber respectively; and F = flow rate of sea water through the chamber. Particle concentration was determined with an electronic particle counter (Coulter Electronics model TAII) equipped with a 50 μm aperature.

RESULTS

The composition of summer photosynthetic picoplankton from coastal surface waters (Table 1) includes the procaryotic picophototrophs (cyanobacteria) at $1–5 \times 10^5$ cells ml^{-1} and eucaryotic picophototrophs (picoalgae) at $0.2–1 \times 10^4$ cells ml^{-1} (Johnson and Sieburth 1982, Joint and Pipe 1984, Murphy and Haugen 1985). These phototrophic types are typically 1–10% of the total bacterial population by numerical abundance ($1–3 \times 10^6$ cells ml^{-1}). In water samples taken on 2 July 1985, however, cell counts by epifluorescence microscopy revealed an unprecedented population of picoalgae at 9.3×10^5 cells ml^{-1}. In the 29 July sample, epifluorescence counts of picoalgae indicated that their populations had decreased 20-fold within 4 weeks, thus indicating a waning of the bloom. Total bacterial counts, although still elevated in comparison to non-bloom summers, had also declined during this period. The abundance of cyanobacteria in this sample, 6×10^4 cells ml^{-1}, remained about the same as during peak bloom conditions.

Transmission electron microscopy was used to elucidate the changes in the composition of the photosynthetic picoplankton. From analyses of TEM preparations from the 2 July water sample, the composition of the photosynthetic picoplankton was found to be dominated (>95% by numerical abundance) by a single cell type at 9.27×10^5 cells ml^{-1}. This organism, named *Aureococcus anophagefferens* is a hitherto undescribed Chrysophyte that is being placed in a new genus (Sieburth et al. 1988). In the 29 July sample, TEM micrographs (Figure 1) revealed a variety of pico-sized photosynthetic organisms including the usual summertime dominant, *Synechococcus*, the dominant bloom algae, *Aureococcus*, and other eucaryotic cells

TABLE 1.

Relative composition of phototrophic types in the summer coastal picoplankton in typical years and during the 1985 brown tide's peak (2 July) and late bloom (29 July) phases.

Taxonomic category	Abundance (cells ml^{-1}) Non-bloom summers	Peak bloom 1985	Late bloom 1985
Procaryotic picophototrophs (cyanobacteria)	$1–5 \times 10^5$	4.9×10^4	6.2×10^4
Eucaryotic picophototrophs (picoalgae)	$0.2–1 \times 10^4$	9.3×10^5	5.1×10^4
Total bacteria	$1–3 \times 10^6$	1.2×10^7	8.0×10^6

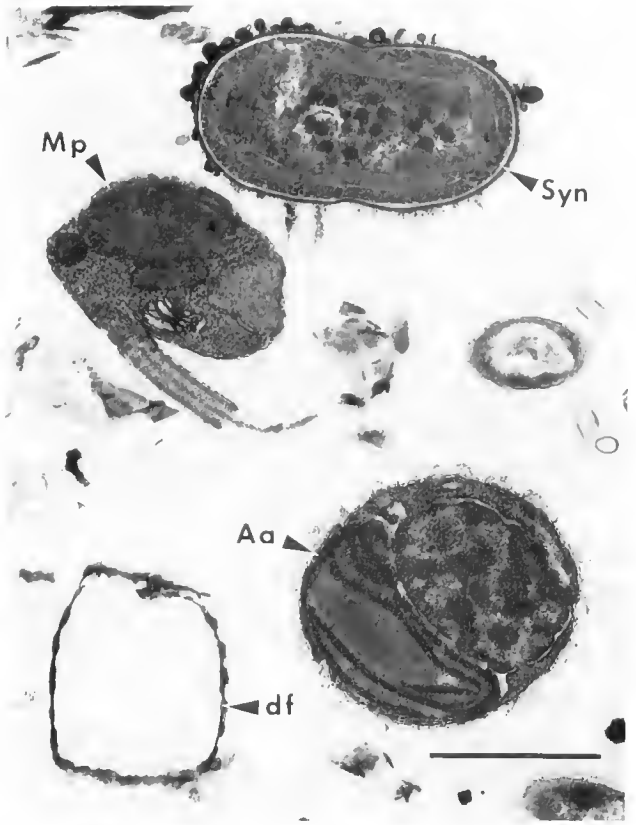

Figure 1. Ultrastructural comparison of the components of coastal photosynthetic picoplankton by transmission electron microscopy of thin sections (sample taken at the end of the 1985 brown tide bloom). The cyanobacterium *Synechococcus* (Syn) and the picoalga *Micromonas pusilla* (Mp) were replaced during the bloom by the new picoalga species *Aureococcus anorexefferens* (Aa). Picodiatoms (probably *Minutocellus polymorphus*) were also present at the end of the bloom as shown by an empty frustule (df). Marker bar equals 1.0 μm.

such as the prasinophyte, *Micromonas pusila* and a picodiatom frustule (probably *Minutocellus polymorphus*). From this micrograph, it is evident that a variety of similarly-sized but morphologically distinct species are present. Only with the aid of TEM was cell differentiation among these similarly-sized chlorophyll-containing picoalgae possible.

The effect of picoplankton species composition on one aspect of mussel nutrition was tested by comparing the feeding rate of mussels on two diets, *Synechococcus* and bloom algae dominated by *Aureococcus* (NBP). Feeding rate was inferred from the rate of removal of particles from suspension. Although the retention of particles by the filtration apparatus of the mussel is markedly influenced by size (Vahl 1972), the two food types were of equivalent diameter (Figure 2), such that dietary effects on feeding rate due to differences in particle capture efficiency were minimized.

Both diets were fed to mussels at cell concentrations up to that of the bloom (1×10^6 cells ml^{-1}). When NBP was diluted to a concentration of about 10% of the bloom, there was some clearance, but almost none was observed at bloom concentrations (Figure 2). In contrast, clearance rates of *Synechococcus* were higher than NBP over a similar range of cell densities. The rates of clearance observed on the *Synechococcus* diet compare favorably with that of Lucas et al. (1987), who observed weight-specific clearance rates of 24.6–38.7 ml min^{-1} for 4.8 cm length (1.3 g dry weight) *M. edulis* fed natural particles from 1.5–2.5 μm in diameter. Thus, feeding on *Synechococcus* was apparently optimal, whereas the removal of NBP from suspension appeared inhibited. From these results, it is probable that feeding activity of mussels in Narragansett Bay was significantly suppressed during the bloom.

DISCUSSION

Studies of the contribution of bacterial-sized organisms to the nutrition of bivalves have shown that the biomass and nutritional content (i.e., C:N ratio) of this component of the plankton are often sufficient to support the dietary requirements of the animal (Seiderer et al. 1982). However, the optimization of this potential food resource may be limited by the size of particles which can be efficiently retained by the filtration system (Seiderer and Newell 1985, Amouroux 1986, Lucas et al. 1987). In *M. edulis*, a marked decline in retention efficiency occurs for particles <4 μm diameter (Vahl 1972, Jorgensen 1975), although at 2.0 μm in diameter, retention efficencies of 82.4% have been observed (Lucas et al. 1987).

Obtaining adequate nutrition from bacterial-sized particles also depends upon the ability to produce the necessary digestive enzymes (McHenery et al 1979, McHenery and Birkbeck 1982, Seiderer et al. 1982). This does not appear to be problematic for *M. edulis*, since this species has been observed to efficiently digest several species of bacteria (Prieur 1981, Birkbeck and McHenery 1982). Thus, under the bloom conditions of the 1985 "brown tide" in Narragansett Bay, one would expect that the abundance of particles would satisfy the nutritional requirements of mussels. This bloom was not well tolerated by *M. edulis*, however, as 30–100% mortality was observed in mussel beds located in different areas of Narragansett Bay (Tracey 1985). In addition, long-range impacts of the bloom on Narragansett Bay are evident given a virtual lack of larval settlement until the summer of 1987 (Tracey in press).

The effect of the bloom on mussels is attributed to the reduction in feeding which occured when the composition of the photosynthetic picoplankton shifted from the cyanobacterium *Synechococcus* to the picoalga *Aureococcus*. *Aureococcus* does possess an exocellular layer of polysaccharide-like material (Figure 1) which may have caused the reduction in feeding by interfering with the beating of the mussels' gill cilia either mechanically through clogging or chemically by compounds unpalatable or paralytic to the

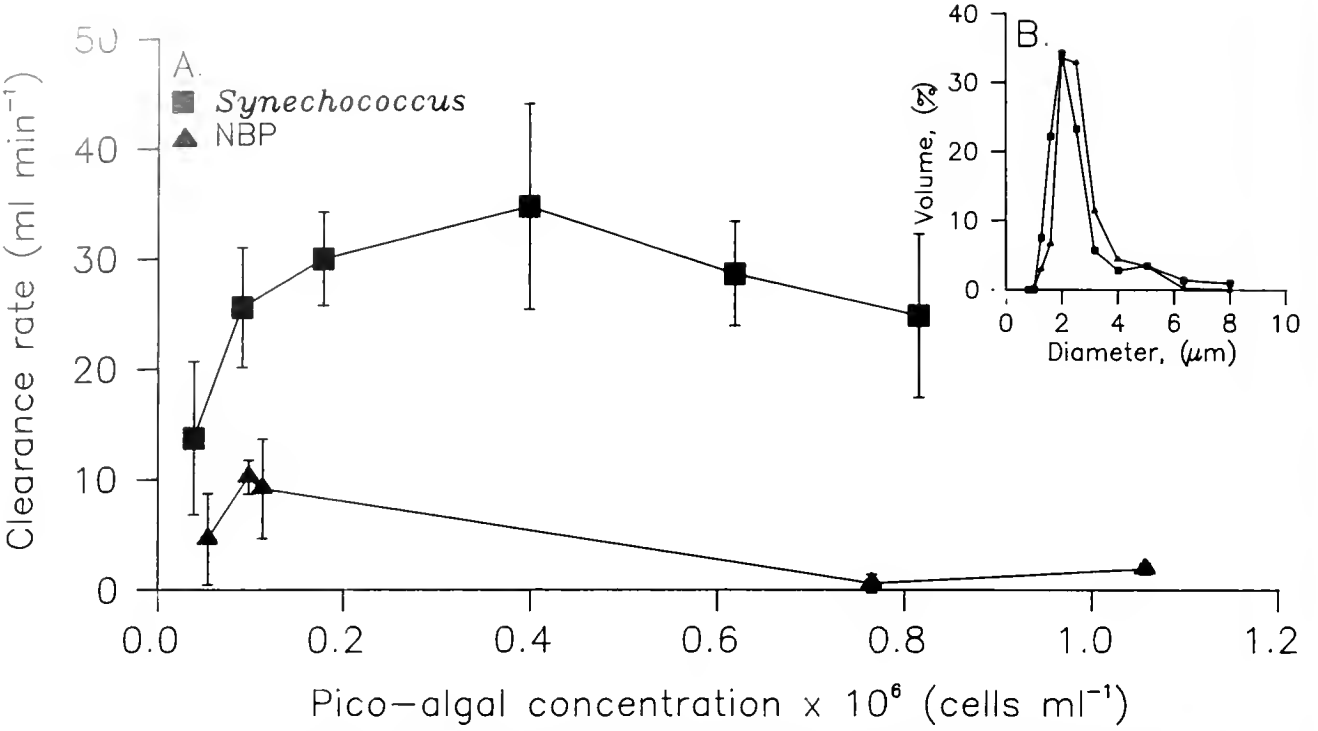

Figure 2. A. Clearance rates (mean ± s.d.) of *Mytilus edulis* on differing concentrations of two similarly sized phototrophs; *Synechococcus* and Narragansett Bay picoplankton (NBP) dominated by *Aureococcus*. B. Size-frequency distribution of the two particle types.

feeding apparatus. Such mucilaginous covers are common to freshwater blue-green algae and have been found to act as a defense to predation by zooplankton (Porter 1976). The starvation condition caused by the non-feeding behavior was probably exacerbated by the blooms' persistence during the time of mussel spawning (Tracey in press), a period when the bulk of available energy is committed to reproductive processes (Bayne 1975). It is believed that a combination of these factors was sufficient to cause the observed population level effects (Tracey in press).

Although we believe that the dominant "brown tide" organism, *Aureococcus*, was primarily responsible, other species may have been present which could cause reduced feeding when their concentrations greatly exceed their normal abundance. Concurrent to the bloom in Narragansett Bay the "brown tide" occured in the coastal embayments of Long Island during 1985 and again in 1986 to an extent which caused the demise of both eel grass beds (Dennison 1986) and scallop populations (Bricelj 1987). Prior to these events, a decline in the oyster fishery of Moriches and Great South Bay of Long Island was observed during a shift in the composition of phytoplankton towards the seasonal dominance of the picoplankters *Nannochloris atomus* and *Nannochloropsis salina* (Ryther 1954). However, in that event, the poor food quality of *Nannochloris* may have been related to the inability of scallops to digest these cells (Bricelj et al. 1984), rather than a reduction in feeding. In contrast, the results with *Synechococcus* reported here and in other studies examining feeding on natural particulates suggest that other picoplankton-sized particles either have no effect or may significantly contribute to the nutrition of bivalve molluscs (Wright 1982, Siederer and Newell 1985, Lucas et al. 1987). For these reasons, further study of the species composition of algae within the picoplankton size range is required, as it may have dramatic effects on the nutrition of bivalve molluscs.

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MEASURING THE ECONOMIC EFFECTS OF BROWN TIDES

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ABSTRACT This paper develops behavioral models for examining the reactions of marine resource users to reduced resource quality associated with brown algal blooms. Models of recreational and commercial fishing are developed, as well as other recreational uses. These models emphasize the concept that the presence of brown tides at certain sites will cause the commercial and recreational activity to substitute of other sites and other species. These substitutions will have additional implications for economic welfare. After developing the conceptual models, preliminary estimates of economic losses are made for the bay scallop fishery. Annual economic losses are of the order of two million dollars.

KEY WORDS: economic losses, fishery economics, bay scallops, brown tides

INTRODUCTION

The presence of brown tides in coastal embayments in New York and surrounding states has caused a great deal of concern among resource managers, the scientific community, and the marine resource utilizing public. The marked difference between embayments which are affected with brown tides and embayments which are unaffected (but by no means pristine) is largely responsible for this reaction.

Natural scientists have begun to document the biological effects of brown tides, but little work has been done on the economic effects associated with these ecological changes. The current level of information concerning brown tides, their biological impacts, and the economic utilization of marine resources is not capable of supporting the quantification of all the economic impacts. This paper does not attempt this, but does try to shed some light on this issue by proceeding in the following directions. First, economic theory is used to discuss the nature and the likely orders of magnitude of the various economic impacts of brown tides. Second, economic models are developed in anticipation of data which will enable their estimation. Third, preliminary estimates are made of one component of the losses from brown tides, those realized in the bay scallop fishery in New York.

Defining the Economic Losses

Since this paper is addressed to an interdisciplinary audience, the discussion of economic losses will begin by presenting the definition of net social benefits which is universally employed by economists. The net social benefit of any good, service activity or resource is simply equal to how much people value it less the opportunity cost of obtaining it. This measure of net benefits is portrayed graphically in Figure 1. For example, let the good be bay scallops, let π_1 represent the aggregate marginal willingness to pay for the good, and let MC_1 represent the marginal cost of the good. Q_1 would represent the equilibrium quantity and P_1 the equilibrium price.

The area under π_1 (from 0 to Q_1) represents the total value of the good, while the area under MC_1 represents the total opportunity cost of the good. The area between the two (area ABC) therefore represents the net social benefits of bay scallops. This area is divided by economists into consumers' surplus (area ABP_1) and producers' surplus (area P_1BC).

If brown tides adversely affect bay scallops then the economic losses would be area ABC if the brown tides completely eliminated the organism. If it depleted the organism by some lesser amount, then the effect would be to shift the marginal cost function leftward. This is depicted as MC_2 in Figure 2. The marginal cost function shifts leftward because the costs of harvesting an additional pound of bay scallops will rise as there are now fewer scallops in the bay to harvest. The loss in economic benefits associated with the depletion of the organism is area DEBC. Of course, if the stock was depleted by such a large amount that it shifted the marginal cost curve so that it was entirely above the willingness to pay function, then that would be economically equivalent to the complete elimination of the stock.

In defining economic benefits, it is important for the non-economist to realize that what the layman thinks is the appropriate measure of economic benefits has no relation to the definition above. For example there are two reasons why economic benefits are not equal to the total amount of money spent on scallops. First, total expenditures does not incorporate the fact that some people may value the good above its market price. Second, it neglects to consider the opportunity cost of the resources used to harvest the scallops.

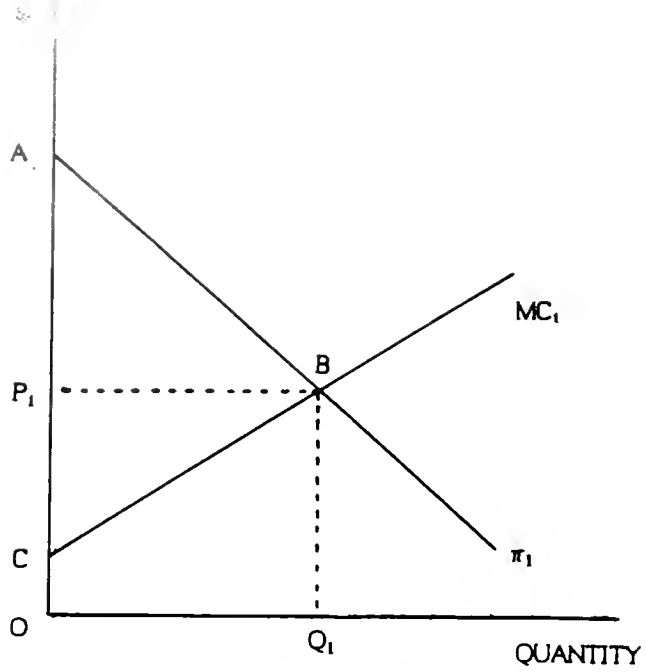

Figure 1. Net benefits.

Economic Loss in Commercial Fishing

There are two primary effects of brown tides on commercial fishing. First brown tides have direct impacts on both shellfish and finfish. Shellfish species such as bay scallops have declined dramatically in direct correlation with the presence of brown tides. Anecdotal evidence also suggests that finfish may leave areas that are affected by brown tides. Both of these effects will directly impact the markets for these species, by shifting the marginal cost curve up and to the left as explained above and diagrammed in Figure 2. The second effect is the indirect effect of brown tide in that adverse conditions in one fishery may lead to adverse effects in another fishery as fishermen switch from species such as bay scallops which are affected by the brown tides to regions and species which are unaffected. The movement to other fisheries can cause overexploitation of those fisheries, which would reduce the economic benefits derived from those fisheries.

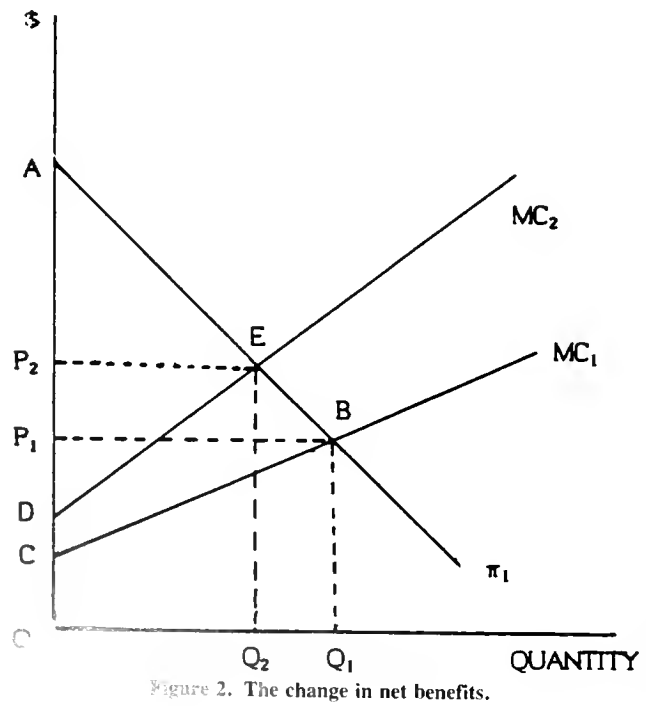

Figure 2. The change in net benefits.

The direct effects of brown tides on a fishery can be derived using models of bioeconomic equilibrium, which have been developed in previous papers (Kahn and Kemp 1985, Kahn 1987). These models call for the estimation of the three equation model below, where equation 1 represents the average cost of catching a unit of fish, equation 2 the inverse demand (willingness to pay) for the fish and equation 3 represents the equilibrium catch equation. C represents the level of catch, X is the level of the stock, ρ_1 is a vector of input prices (labor, energy, etc.), p_s represents a vector of substitute good prices, r represents the intrinsic growth rate of the species, and K the carrying capacity of the ecosystem. Notice that an average cost function has been defined rather than a marginal cost function. This is because in an open access fishery, fishermen respond to individual marginal cost which is equal to fishery average cost. Fishery marginal cost may be derived from the fishery average cost function.

In Kahn's paper, a variety of methodologies are suggested for actually estimating such a model, but most are not applicable to bay scallops due to a lack of time series data on bay scallop stocks and water quality parameters. However, a two equation model (holding the equilibrium catch equation fixed) can be formulated using a proxy for population as a right hand side variable in the average cost function. Such a model was actually estimated using annual data on New York landings of bay scallops for the period 1963–1984. The proxy for population was calculated as a weighted average of past landings. The definition of this variable is presented in equation 4.

$$\text{BSPOP} = \frac{1}{6}[3(C_{t-1}) + 2(C_{t-2}) + C_{t-3}] \qquad (4)$$

The supply function which is estimated is presented in equation 5, with t-statistics in parentheses. This can be inverted (with respect to C and P) to return the fishery average cost function. The lefthand side variable is the quantity supplied (catch). Right hand side variables include the lagged price of bay scallops (P_{t-1}), the proxy for bay scallop populations (BSPOP) and the hourly wage in manufacturing in New York. Lagged price, rather than current price, is used as an explanatory variable because the number of fishermen in the current year is dependent primarily on expected economic conditions in the current

year, and the best proxy for expected conditions is last years' conditions. The hourly wage in manufacturing is included to serve as a control for the opportunity costs of the bayman's time. Although manufacturing is not necessarily the employment that a bayman would chose when displaced from fishing, the wage in manufacturing will be correlated with the wage in construction, agriculture. etc., so it will serve as a reasonable proxy for the opportunity costs of the bayman's time. Equation 5 is estimated using ordinary least squares regression. All estimated coefficients have the correct sign and are statitically significant.

$$\underset{}{Q_s} = \underset{(2.413)}{3613.56} + \underset{(1.745)}{284P_{t-1}} + \underset{(2.460)}{.521POPX} - \underset{(-2.457)}{1284WAGE}$$
$$\text{F-statistic}(4,17) = 5.598 \qquad R^{-2} = 0.408 \qquad (5)$$

The estimated demand function is presented as equation 6. This function is estimated in log–linear form to account for possible nonlinearities in willingness to pay for bay scallops. Linear specifications were also tested, but the log–linear specification performed best. The left hand side variable is the natural logarithm of catch (lnC) and the right hand side variables include the natural logaritm of current price (lnP), the CPI for meat, poultry and fish (lnMPF), New York per capita income and a dummy variable (DPOPE). The dummy variable was included to control for taste changes generated by the relaxation of the Catholic ban on eating meat on Fridays, which Bell (1968) found to have a statistically significant effect on demand for fish in general. The index for meat poultry and fish was included as a substitute good, while income was included as a factor potentially affecting demand. All estimated coefficients were of the expected sign and statistically significant.

$$\underset{}{\ln Q_d} = \underset{(-2.433)}{-34.841} - \underset{(-3.826)}{1.638\ln P_t} + \underset{(2.890)}{5.06\ln}$$
$$\text{INCOME} + \underset{(1.665)}{2.508\text{lnMPF}} - \underset{(-3.412)}{1.187\text{lPOPE}}$$
$$\text{F-statistic}(5,16) = 10.43 \qquad R^{-2} = 0.654 \qquad (6)$$

The next step is to use these equations to compute the economic losses associated with brown tides. The assumption is made that if brown tides continue according to their 1985 and 1986 distributions, the bay scallop populations in Long Island waters will be eliminated.

The first step in this process is to convert the above functions to their inverses. Equation 5 is inverted into an average cost function, and all right hand side variables are set equal to their means with the exception of catch. This function is presented as equation 7. Equation 6 is inverted into a willingness to pay (inverse demand function), and all right hand side variables with the exception of catch are set equal to their mean levels. The transformed equation is presented as equation 8.

$$\pi = 42.78C^{-0.6106} \qquad (7)$$

$$AC = -0.0568 + \frac{1}{284}C \qquad (8)$$

The right hand sides of equations 7 and 8 are then set equal to each other and solved for the equilibrium level of catch. This is 353,000 pounds of bay scallop meats. A marginal cost function (equation 9) is then derived from the average cost function, and consumers' and producers' surplus are computed according to equation 10.

$$MC = -.0568 + \frac{2}{284}C \qquad (9)$$

$$\int_0^{353} (\pi - MC)dC \qquad (10)$$

The solution to the integral in equation 10 represents the economic benefits derived from the bay scallop industry, or the losses to be incurred if brown tides eliminate this fishery. This value is equal to $1.99 million in 1984 dollars ($658,000 in 1967 dollars).

As indicated earlier, there will also be indirect effects upon other industries, as fishermen leave the bay scallop fishery to enter into other fisheries (both finfish and shellfish). There could be additional welfare losses associated with such a movement, as these other fish stocks become subjected to additional fishing pressure. Conversely, the welfare losses could be mitigated if there are possibilities for fishermen to switch to harvesting underutilized species. Although the estimation of these indirect effects is beyond the scope of this paper, we present a methodology with which to do this.

The conceptual model of vessel switching behavior for multiple species is based on the assumption that vessels are profit maximizers and choose their level of effort and species catch subject to their production function technology (ability to combine inputs to produce an output) and species abundance as well as any constraints on inputs or outputs.

Consider a fishing vessel's profit maximization problem subject to quantities constraints:

$$\max_{x,q} p'q - r'x \qquad (11)$$

$$\text{subject to } F(q(\bar{I}),x) = 0, \ \bar{q} \geq q \geq 0, \ \bar{x} \geq x \geq 0$$

where x and q are $k \times 1$ and $M \times 1$ vectors of inputs and outputs respectively, and x and q are upper quantity limits or quota limits on catch. I is a $k \times 1$ vector of measures of species abundances which we assume are fixed. The production function F is an increasing function of q's and a decreasing function of x's. Other standard regularity conditions on F such as differentiability and strict quasi concavity are assumed. These conditions have to do with the smoothness, slope and shape of the function and ensure that a maximum does indeed exist and we do not choose a minimum. Species catch q, is increasing in species abundances, I.

Fishermen face a large number of species which they may catch and a large number of inputs which they may use. However, in most cases we assume they allocate their resources (i.e., effort through their labor and capital) in an optimal way so that the number of species, the amount of each species they are fishing and the amount of inputs they are using constitute their profit maximizing production regime. Let us consider one such regime for a vessel. Since this regime is optimal for that vessel in terms of maximizing profits we denote the vector of inputs and outputs with stars.

$$x^* = (0, x_2^*, \ldots, x_k^*)' \text{ and } q^* = (\bar{q}_1, 0, q_3^*, \ldots, q_m^*)' \tag{12}$$

In this production regime, the first input is not utilized, the first output is produced at the quota level, and the second output is not produced at all.

The Langrangean function is:

$$L = p'q - r'q + \lambda(0\text{-}F(q(\bar{I}),x)) + \phi'q + \psi'x + \bar{\delta}'(q - q) + \bar{\omega}'(x - x) \tag{13}$$

where ϕ, ψ, δ, and ω are vectors of Langrange multipliers. This regime is characterized by the following Kuhn-Tucker conditions:

$$-r_1 - \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial x_1} + \psi_1 = 0 \quad \psi_1 \geq 0; \tag{14}$$

$$-r_i - \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial x_i} = 0 \qquad i = 2, \ldots, k \tag{15}$$

$$p_1 - \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial q_1} - \delta_1 = 0 \qquad \delta_1 \geq 0 \tag{16}$$

$$p_2 - \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial q_2} + \phi_2 \geq 0 \tag{17}$$

$$p_j - \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial q_j} = 0 \qquad j = 3, \ldots, m \tag{18}$$

$$F(q^*(\bar{I}),x^*) = 0 \qquad q^* \geq 0 \qquad x^* \geq 0 \tag{19}$$

Based on recent work by Wales and Woodland (1983) and Lee and Pitt (1986) we introduce the notion of virtual prices. Virtual prices may be thought of as simply those prices which support the vector of profit maximizing production outputs and inputs for the vessel that we observe. Define the virtual price ξ_{d1} for input 1 and virtual price ξ_{s1} for output 1 and ξ_{s2} for output 2 at $(x = 0, \bar{q}, 0)$ as

$$\xi_{d1} = -\lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial x_1} \tag{20}$$

$$\xi_{s1} = \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial q_1} \tag{21}$$

$$\xi_{s2} = \lambda\frac{\partial F(q^*(\bar{I}),x^*)}{\partial q_2} \tag{22}$$

Since $(\partial F(q^*(\bar{I}),x^*)/\partial x_1) < 0$ and $(\partial F(q^*(\bar{I}),x^*)/\partial q_1) > 0$, and $(\partial F(q^*(\bar{I}),x^*)/\partial q_2) > 0$ and ξ_{d1}, ξ_{s1}, and ξ_{s2} are strictly positive, it follows that $\psi_1 = r_1 - \xi_{d1}$, $\delta_1 = p_1 - \xi_{s1}$, and $\phi_2 = p_2 + \xi_{s2}$

Therefore this production regime is characterized by

$$\begin{array}{lll} r_1 \geq \xi_{d1} & 0 < x_i^* < \bar{x}_i & i = 2, \ldots, k \\ p_1 \geq \xi_{s1} & 0 < q_j^* < \bar{q}_j & j = 3, \ldots, m \\ p_2 \leq \xi_{s2} & 0 < q_j^* < \bar{q}_j & j = 3, \ldots, m \end{array}$$

The virtual prices are intuitively appealing in that they may be thought of as shadow prices. Shadow prices reflect the real cost of unpriced goods, either inputs or outputs. Input 1 is not used because the market price is too high. Output 1 is produced up to the quota limit because the market price is even greater than it would have to be to encourage greater output. On the other hand, q_2 is not produced because the virtual price is too high, that is the price at which that vessel would have an incentive to catch that species is higher than the market price.

The use of virtual prices allows us to characterize any number of different production regimes for different vessels. By specifying those production regimes that occur for the vessels in the region we can then determine the probability of vessels switching into another regime based upon their explanatory variables. These variables would include individual vessel characteristics such as horsepower, gear type, boat length, etc. Using the estimated parameters from an econometric model we can then simulate the effects of an exogenous change (such as brown tide) on vessel switching behavior. As we drive the stock abundance level of a fishery down, the model will provide estimates as to how vessels will move into other fisheries.

Economic Losses in Recreational Activities

One of the more important contributions of the field of environmental and resource economics over the last two decades has been the development of models with which one can value environmental resources used in recreational activities. The predominant model used in policy analysis has been the travel cost demand model. The model is built upon prices that an individual faces for visiting a recreational site including mileage costs, other access costs at the site (such as entrance fees, fares or parking fees) and opportunity costs of time travelling to and from the site, as well as time spent at the site.

Using these prices and visits to the site, one can estimate a travel cost demand function, and estimate how changes in environmental quality shift the demand function and change the social benefits associated with the activity (Bockstael, Hannemann and Strand 1982). Several studies

have been done of different activities in different regions which indicate that small improvements in environmental quality can lead to significant increases in social benefits. These studies include Samples and Bishop (1985), Strand, Bockstael and Kling (1986), Smith, Desvouges and Mcgivney (1983) and Clark and Kahn (1988).

Unfortunately, the data with which to estimate such models for Long Island swimming, fishing and boating do not exist. Although data have been collected by Kahn with Sea Grant and New York Department of Environmental Conservation for recreational fishing on Long Island these data are not yet in a form where such models can be estimated. However, it is possible to make some inferences about the likely magnitude of such impacts based on principles of economic theory.

The major point that can be made is that the economic impacts of brown tides on recreational activity are likely to be quite small if the brown tides affect only a small number of recreational sites. The losses are not simply proportional to the amount of brown tide, but are likely to increase at an increasing rate. The reason for this is that when the number of sites affected by brown tides is small, there are many substitute sites available. Economic theory suggests that the more substitutes for a good, the flatter the demand curve and the less consumer surplus associated with the good or site. The economic losses of brown tides in this case would consist of slightly higher travel costs to go to a different (unaffected site) as well as more congestion associated with the unaffected sites. However, as the number of affected sites grows, the number of substitute sites diminishes. The consumers' surplus associated with an unaffected site becomes large, and the loss of that site to further incursions of brown tides becomes increasing more costly.

This is not to say that there will not be important local economic impacts. For example, if brown tides increase in the Peconic Bay region of Long Island, there will be a drop in the regional income of that area as potential swimmers, boaters and anglers go to other embayments, the ocean, or freshwater sites. However, it should be noted that this loss in regional income is not a loss to society as a whole, but merely a transfer from one region to another as expenditures and therefore income increases in other regions due to the change in recreational patterns.

Property Value Changes

The presence of brown tides is likely to cause declines in property values of waterfront property in the affected areas (although these declines may only be relative in the Long Island housing market.) These declines do not reflect losses in themselves; they merely are the capitalized values of other losses in recreational fishing, boating, and other water dependent activities. If all these other values could be measured, this would simply be a double counting of the losses. George Parsons (1986) provides an excellent account of the conditions under which housing values are likely to capture the effects of changes in the quality of the resource.

Hedonic housing price methods rely on explaining the variation in housing prices as a function of the house and neighborhood characteristics including water quality of adjacent or nearby water bodies. However, for the Long Island housing market it may be difficult to isolate this effect since the demand for waterfront property has been increasing due to socioeconomic changes, and the availability of waterfront property has decreased due to land use restrictions and the fixed amount of coastline.

CONCLUSIONS

The current level of information concerning brown tides, their biological impacts, and the economic utilization of marine resources is not capable of supporting a statistically significant quantification of all the economic impacts. This paper tries to shed some light on this issue by making the following contributions. First, economic theory is used to discuss the nature and the likely orders of magnitude of the various economic impacts of brown tides. For most recreational activities, this is likely to be small, unless the presence of brown tides increases dramatically. Second, economic models are developed in anticipation of data which will enable their estimation. Both models of bioeconomic equilibrium and species switching are demonstrated to be likely candidates. Third, preliminary estimates are made of one component of the losses from brown tides, those realized in the bay scallop fishery in New York. These are shown to be in the neighborhood of two million dollars per year.

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EFFECTS OF AN ALGAL BLOOM ISOLATE ON GROWTH AND SURVIVAL OF BAY SCALLOP (*ARGOPECTEN IRRADIANS*) LARVAE

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ABSTRACT Some aspects of the nutritional value of *Minutocellus polymorphus*, a 2.5–3.5 μm diatom isolated from algal blooms implicated in the devastation of scallop populations of eastern Long Island, New York, were assessed. Growth in shell length, grazing rate, absorption efficiency and survival of bay scallop (*Argopecten irradians*) larvae, were determined in laboratory cultures fed this bloom isolate and the Tahitian strain of *Isochrysis* sp. Absorption efficiency was determined using a dual radiotracer method in which algae were labeled with both ^{51}Cr and ^{14}C. Survival was not significantly affected by algal diets. The type of algal species affected the growth of early larvae while growth of later larvae was affected by algal cell concentration. Early larvae absorbed less carbon from *Minutocellus* than from Tahitian *Isochrysis*. Grazing rates on *Minutocellus* were comparable to those on *Isochrysis* until metamorphosis was completed at which point *Isochrysis* was grazed at a greater rate than *Minutocellus*. The results suggest that a qualitative aspect, possibly a relatively low digestibility, of the *M. polymorphus* diet resulted in larval mortalities and widespread recruitment failure.

KEY WORDS: *Minutocellus polymorphus*, *Argopecten irradians*, picoplankton, bloom, larvae

INTRODUCTION

The bay scallop, *Argopecten irradians* (Mollusca:Pectinidae) is a suspension-feeding bivalve mollusc indigenous to coastal estuarine waters of North America (Belding 1931, Rehder 1981). In New York, locally important, commercial fishery for the species exists primarily in the Peconic-Gardiners Bays estuary of Long Island. The 1984 bay scallop harvest from the Peconic-Gardiners Bays area was valued at $1.26 million (New York State Department of Environmental Conservation, Fisheries Statistics 1984). Bay scallop population sizes experience a large degree of interannual variability (U.S. Department of the Interior 1981, see also Ingersoll 1886) which is attributed to the species' short life span and semelparous reproductive cycle (Gutsell 1930, Belding 1931). Bay scallops generally spawn only once during their life cycle, this occurring before the end of their first year. Bay scallop populations are thus composed of only one year class; two year old animals are rare exceptions (Belding 1931). The planktotrophic, planktonic larvae remain in the water column for 10–19 days (Castagna and Duggan 1971) and settle, attach and complete metamorphosis on suitable substrates such as eelgrass, *Zostera marina* (Belding 1931). Should conditions be unfavorable for larval recruitment in any year, the following season's scallop harvest, entirely dependent on the previous year class, may be extremely poor.

A phytoplankton bloom is an example of an oceanographic condition which can affect bivalve larval recruitment. The coastal embayments of Long Island have a history of recurrent phytoplankton blooms (Ryther 1954) which may have been one of the primary factors which led to the demise of the once prosperous oyster industry in the area. Plankton samples collected in June, 1985, from Northwest Harbor, Long Island, New York (Figure 1) as part of a New York Sea Grant Institute-funded research program on bay scallop larvae, showed that abundances of bivalve larvae (>150 μm) declined dramatically throughout the summer, concurrent with a picoplankton bloom (Cosper et al. 1987). Spat collectors presenting several substrate types gathered no bivalve postlarvae throughout June–August, 1985; in fact, few fouling organisms of any type were found. This apparent failure of bivalve larval recruitment accompanied by an intense picoplankton bloom (up to 2000 cells · ml^{-1}) presented a unique opportunity to study how such oceanographic phenomena affect the growth and survival of bivalve larvae.

The objective of this study was to assess the effect of a microalgal species isolated from the 1985 Long Island bloom on the growth and survival of bay scallop larvae. Possible mechanisms for effects on growth and survival were investigated by measuring grazing rates and absorption efficiencies of larvae feeding on the isolate.

The degree to which a particular algal diet supports growth in bivalve larvae may be influenced by either the quality of the alga (nutritional contents, cell size and shape, digestibility) or the quantity of algal cells provided. Toxic metabolites produced by the algal cells or the toxicity of the cell contents are also possible factors affecting the value of an algal species as food for bivalve larvae (Bayne 1983).

The fact that some microalgal species are more suitable than others as food for bivalve larvae has been well documented (Davis and Guillard 1958, Walne 1963, Newkirk and Waugh 1980). Pechenik and Fisher (1979) state that the

> "value of an algal species as a food depends upon 1) the ability of the zooplankton organism to ingest it, i.e., on cell size and shape, 2) the accessibility of the cell contents to

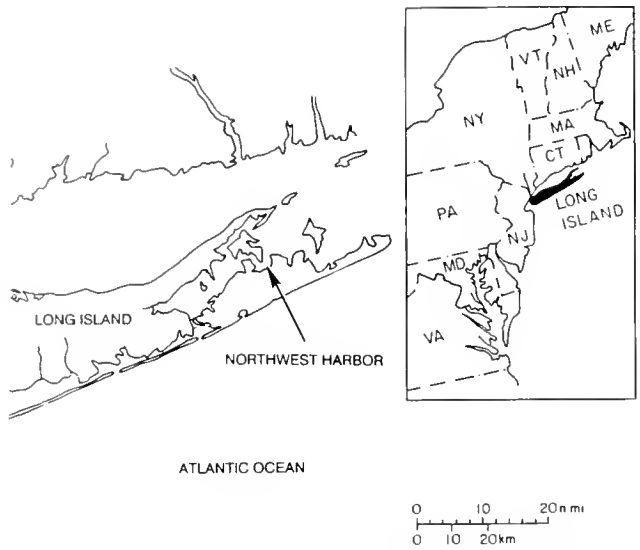

Figure 1. Location map for Northwest Harbor on Long Island, New York.

> the herbivore's digestive system, and 3) the ability of the phytoplankton species to provide the organism with nutrients essential for growth and development."

In this study the first two criteria of food value (ability of the organism to ingest and digest the food) are addressed. The role of specific essential nutrients in the nutritional value of certain algal species has been addressed in a number of studies (Waldock and Nasciomento 1979, Langdon and Waldock 1981, Chu et al. 1982, Langdon 1983), however, the biochemical analyses and biochemically defined diets needed for such experimentation were not within the scope of this study.

Cell Size and Shape

Veliger larvae concentrate suspended particles for ingestion using an opposed cilia band system (Strathmann and Leise 1979, Strathmann et al. 1972). Rather than the cilia acting as a sieve, the individual cilia are presumed to intercept the particles, pushing particles faster than the water around them by way of some sort of weak adherence of particle to cilium. There probably is no minimum particle size limit below which particles are too small to be captured by bivalve larvae (Strathmann et al. 1972), however, many investigators do report an optimum range of particles captured with the greatest efficiency (Walne 1965, Wilson 1979, 1980, Riisgard et al. 1980, Fritz et al. 1984, Sprung 1984a).

Digestibility

Other investigators have emphasized the importance of digestibility in assessments of the nutritional value of microalgae in bivalve larval diets (Chu et al. 1982). Interspecific differences in digestibility exist for many species of microalgae. As food for bivalve larvae, naked flagellates have been found to be superior to algae with rigid, cellulose cell walls, the assertion being that cell walls inhibit the digestive capability of the larvae (Walne 1965, Davis and Guillard 1958, Babinchak and Ukeles 1979).

Quantity of Algal Cells

Much work has been done on the important relationship between larval growth rate and algal cell concentration {reviewed by Bayne (1983) and Sprung (1984b)} as well as grazing or clearance rate and algal cell concentration (reviewed by Sprung 1984a). For example, Walne (1965) found that *Ostreas edulis* larvae fed *Isochrysis galbana* grew maximally at algal cell concentrations of 50 cells/μl. During the picoplankton bloom of 1985, bivalve larvae in the waters of the Peconic and Gardiners Bay estuary experienced persistent concentrations of phytoplankton cells in excess of 2000 cells · ml^{-1}. Many investigators have reported that such high algal cell concentrations reduce larval feeding rates and growth (Sprung 1984b, Wilson 1979, Malouf and Breese 1977, Rhodes and Landers 1973, Walne 1966, Loosanoff et al. 1953, 1954).

Toxic metabolites associated with high concentrations of microalgae have been implicated as a possible reason for the depressed growth rates seen at supraoptimal concentrations of food (Davis 1953, Loosanoff and Davis 1963, Rhodes and Landers 1973, Sprung 1984a). Mechanical inhibition of larval feeding due to the excess production of pseudofeces in response to high algal cell concentrations was first reported by Yonge (1926) and has been cited as another possible cause for reduced growth rates at such concentrations (Malouf and Breese 1977, Sprung 1984a). Overloading of the larval digestive system has also been suggested as a possible explanation for the observed low growth rates of larval bivalves fed algae at high cell concentrations (Malouf and Breese 1977).

Little is known of the relationship between food concentration and absorption in bivalve larvae. One potential mechanism of response to an overabundance of food is a reduction in absorption efficiency. However, Walne (1965) found that although total assimilation (absorption–excretion) increased with algal cell concentration, even up to very high concentrations, the assimilation efficiency was relatively constant over a wide range of cell concentrations.

MATERIALS AND METHODS

Isolation and Identification of Picoplankton

Discrete, round, brown, unialgal (although non-axenic) colonies of a small (2.5–3.5 μm diameter) centric diatom (isolated from field samples taken at Jessup's Neck, Long Island New York, during July, 1985) grew well on F/2-enriched agar plates (Guillard and Ryther 1962). These colonies were picked individually and used to inoculate sterile culture tubes of F/2-enriched, filtered seawater. Scanning and transmission electron micrographs of this isolate re-

vealed this species to be *Minutocellus polymorphus* (hereinafter referred to as M-POLY) (Siddall et al. 1986). This identification concurred with an earlier, preliminary identification by Greta Hasle (University of Oslo, Norway; personal communication). Other scanning electron micrographs of this bloom isolate and field samples indicated that M-POLY was at least one of the species of algae present in the Bays during the bloom (Siddall et al. 1986).

Early attempts to produce scanning electron micrographs revealed algal cells which were enveloped in what appeared to be a thick sheath of organic material. Attempts to dissolve this refractory sheath by washing in concentrated hydrochloric acid for up to 24 hr. were unsuccessful. Methanol was the only solvent capable of dissolving this sheath (J. Mitchell pers. comm.).

Culture and Radiolabeling of Algae

Algae were cultured following the methods described by Guillard (1974). The Tahitian strain of *Isochrysis* sp. (referred to as T-ISO) was used in growth experiments as a control diet of known value (Ewart and Epifanio 1981) against which growth of larvae fed the bloom isolate could be evaluated. M-POLY seeemed to grow best under constant agitation and lower intensity light than was given other algae grown in the laboratory. M-POLY grew very well in culture most of the time but was unpredictable in cultures larger than 1.5 L. Large, 15 L cultures of M-POLY sometimes failed to grow after inoculation, however when cultures grew well during the first 24 hrs. invariably dense cultures of algae resulted. To ensure a constant supply of large volumes of isolate, semi-continuous rather than batch culture of M-POLY was used when rearing algae for growth experiments. Both species of algae were harvested during the exponential phase of growth ($2.0–7.0 \times 10^7$ cells $\cdot$ ml^{-1}). Phytoplankton cell counts were made on a Coulter Electronics model TA-II electronic particle counter.

The production of radiolabeled algae for use in absorption efficiency experimentation in general followed the methods described by Bass (1983) and Bricelj et al. (1984). Cultures ranging in volume from 150 to 500 ml were incubated with ^{14}C-bicarbonate radiolabel (0.2 μCi/ml) in tightly capped Ehrlenmeyer flasks for five to six days or until the cultures were sufficiently dense to provide enough labeled algal cells to conduct an absorption efficiency experiment. At least 24 hr. before the ^{14}C-labeled algae was harvested, ^{51}Cr in 0.1 N hydrochloric acid (1 μCi/ml of algae culture) was added. The hydrochloric acid was neutralized with an appropriate volume of 0.1 N sodium hydroxide.

Before each experiment, unincorporated radiolabel was washed from the labeled algae by centrifuging the algae and resuspending the cells in unlabeled, filtered seawater. This process was repeated three times. It was assumed that all of the unincorporated radiolabel was removed by this process.

Culture of Larvae

Sexually mature *Argopecten irradians* adults were spawned artificially within two days of collection from the field. Sperm and eggs were collected separately then mixed in a ratio of ~100 sperm cells per egg; on some occasions mass spawning and fertilization was allowed. In such cases, some degree of self-fertilization was inevitable, however, Castagna and Duggan (1971) reported that self-fertilization in bay scallops did not significantly affect the growth or survival of the resultant larvae. Gametes were allowed to commingle for 15–20 min. after which time fertilized embryos were separated from sperm by gently rinsing the embryos with filtered seawater onto a Nitex screen (20 μm mesh). Embryos were reared at 200–300/ml in conically-shaped 15 L polyethylene culture vessels. Veliger larvae were collected on 63 μm Nitex screens and placed in freshly filtered seawater. Except for larvae for growth experiments 1 and 2 which were immediately used in the experiments, larvae were fed 50 T-ISO cells/ml and reared in 15 l cultures (20/ml) or 2 l cultures (2/ml). Cultures were maintained at 22–25°C and 30 ppt. with complete seawater exchanges every 48 hrs.

Grazing Rate Experiments

To determine if the small cell size (2.5–3.5 μm) of M-POLY limited the ability of scallop larvae to capture it, grazing rates of larvae and postlarvae fed M-POLY or T-ISO were measured. Each experiment was conducted with ten 2 L culture vessels: six vessels were stocked at 2 larvae/ml. Four vessels, stocked only with algae, were used as controls to account for algal cell division during the course of the experiment. There were two treatments of algae used in these experiments:

Treatment—50 T-ISO cells/μl
Treatment 2—M-POLY cells/μl

T-ISO (5–7 μm equivalent spherical diameter as reared in our laboratory) is four times as voluminous as M-POLY (2.5–3.5 μm equivalent spherical diameter). On a total cell volume basis, 50 cells/μl T-ISO is equivalent to 200 cells/μl M-POLY. Concentrations providing a total cell volume equivalent to 50 cells/μl T-ISO were considered optimal (10–100 cells/μl according to Sprung 1984b, Gallager and Mann 1980, Walne 1963, 1965, Wilson 1980).

Low larval stocking densities (2/ml) were used to minimize effects on grazing rates observed by other investigators at high larval stocking densities (Fritz et al. 1984, MacDonald in press). There were two controls of each species of algae at the appropriate concentration in seawater during each experiment. These experiments were conducted with larvae and postlarvae from a single spawning of scallops. These animals ranged in shell length

(parallel to the hinge line) from 119 μm larvae to 507.5 μm postlarvae (Table 1). Experiments with veligers and pediveligers lasted from eight to twelve hours; 4.5 to 8 hr. with the postlarvae. Grazing rate determinations were conducted in total darkness to minimize algal cell division.

Triplicate samples of seawater from each culture were taken at initiation and termination of each experiment. Samples were immediately fixed with Lugol's solution and cell concentrations determined using a Coulter Model TA-II electronic particle counter.

The changes in algal cell concentration in experimental cultures were corrected for algal cell divisions observed in control cultures (no larvae). Total numbers of cells grazed per hr. were then calculated from total culture volume. Three estimates were made of age-specific grazing rates for each treatment.

Absorption Efficiency Experiments

The amount of carbon which scallop larvae could absorb from M-POLY or T-ISO relative to the amount of carbon available was determined using the ^{51}Cr:^{14}C dual tracer method for measuring absorption efficiency (Calow and Fletcher 1972). This method was adapted for use with suspension feeding bivalves by Bricelj et al. (1984). Although other methods of directly measuring absorption or assimilation by adult bivalves do exist (see Bricelj et al. 1984), the dual radiotracer method is the most appropriate for bivalve larvae as there is no need to separate feces from food or pseudofeces.

Four 100 ml cultures of scallop larvae (five larvae/ml) were held in 10 cm diameter acrylic chambers with 63 μm mesh Nitex bottoms, placed inside 1500 ml heavy-duty glass beakers. The chambers allowed larvae to be transferred gently to different algal suspensions with minimum disturbance. The chamber was removed from the beaker of algae, gently rinsed of excess algae with filtered seawater, and replaced in a beaker containing a fresh suspension of algae. The suspension was stirred approximately every 30 min. by gently raising and lowering the chamber through the depth of the algal suspension. Larval feces fell or were rinsed through the screen on which the larvae were retained. Larvae used in absorption efficiency experiments were 100 and 121 hr. post-fertilization and 107.6 and 110.9 um in shell length, respectively.

Availability of radiochemicals and difficulties in culturing sufficient quantities of radiolabeled algae, led to variations in experimental concentrations of radiolabeled algae in treatments of the two absorption efficiency experiments. Absorption efficiency experiment 1 was conducted using the following four treatments of dual-labeled algae. The comparative role of each treatment in these experiments (noted in parentheses) is based on Walne's (1965) report that 50 *Isochrysis* sp. cells/μl was "optimal" for *Ostrea edulis* larvae and our own observations of 2000 picoplankton cells/μl in field samples of the 1985 bloom.

Treatment 1 was T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2 was T-ISO at 250 cells/μl (low bloom equivalent)
Treatment 3 was M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4 was M-POLY at 1000 cells/μl (low bloom)

Absorption efficiency experiment 2 was conducted with the following four treatments of dual-labeled algae:

Treatment 1 was T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2 was T-ISO at 500 cells/μl (high bloom equivalent)
Treatment 3 was M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4 was M-POLY at 2000 cells/μl (high bloom)

Preliminary experiments had shown that scallop larvae could pass fluorescent paint particles through their digestive tracts in as little as 30 min. Thus it was assumed that 30 min. was the earliest time at which labeled feces could be collected after larvae were pulse-fed labeled algae.

After actively feeding for 30–35 min. in the labeled algae, the larvae and the chamber were thoroughly rinsed with filtered seawater and placed in a beaker of fresh, filtered seawater stocked with unlabeled algae of the same species and concentration as the labeled treatment. Every 1–2 hr. each chamber of larvae was rinsed and moved to a fresh, unlabeled algal suspension of appropriate cell concentration. Fecal material which passed through the Nitex screen bottom of each chamber was collected by gently filtering the entire volume of algal suspension and associated fecal material onto Nuclepore membrane filters (0.6 μm pore size, 38 mm diameter). Feces were collected over a 7–8 hr. period. A preliminary, 15 hr. dual-tracer experiment demonstrated that 98% of the total recovered non-ab-

TABLE 1.

Description of larvae and postlarvae used in grazing rate determinations.

Experiment	Mean length (μm)	Age (days after fertilization)	Description
1	119	7	veligers
2	168	9	veligers, some pediveligers
3	172	11	onset of metamorphosis
4	189	13	postlarvae, 2–5 ctenidia
5	258	16	2–6 ctenidia
6	361	18	3–6 ctenidia
7	508	24	7–8 ctenidia

sorbed ^{14}C was collected during the first 5 hr. after the larvae were removed from the radiolabeled food.

Before each experiment, samples were taken of each species of radiolabeled microalgae for analysis of the isotopic ratio of the food. Algal samples were gently filtered onto Nuclepore membrane filters (0.6 μm pore size, 25 mm diameter) and rinsed with filtered seawater. The filters on which the food samples and fecal samples were retained were placed individually in plastic counting tubes and immediately measured for ^{51}Cr counts per min. (cpm) on a gamma counter (Beckman model 8000). After gamma counting, each sample was moistened with 0.1 ml distilled water and digested for at least 24 hr. in 1–2 ml of tissue solubilizer (NCS, Amersham). Twelve ml of scintillation cocktail (Econofluor) were then added and allowed to equilibrate with the NCS in the dark for 24 hr. Carbon-14 decays per min. (dpm) were measured with an LKB liquid scintillation counter which had an internal dual-label counting program. The program incorporated a quench correction curve generated with a series of ^{14}C-hexadecane standards quenched to varying degrees with different concentrations of algal cells. With this quench curve the program automatically estimated ^{14}C dpm from cpm. Computer programs were written to convert ^{51}Cr cpm to ^{51}Cr dpm. The dpm of each isotope were summed for all fecal samples gathered during the course of each experiment to calculate the fecal isotopic ratio of ^{51}Cr:^{14}C. The programs made all necessary decay, energy spectrum interference, and background radiation corrections to data and ultimately computed absorption efficiencies.

Calow and Fletcher (1972) state that one of the assumptions of the dual-label method is that ^{51}Cr is not absorbed to any significant extent. A preliminary experiment showed that ^{51}Cr absorption by bay scallop veligers was negligible (~1%). Absorption efficiency was calculated as

$$AE = 1 \frac{\text{food isotopic ratio}}{\text{fecal isotopic ratio}} \times 100\%$$

Growth and Survival Experiments

To measure the effect of a diet of M-POLY on bay scallop larvae, the following five diets of cultured algae were fed to larvae in each of the four longer-term growth experiments (as for absorption efficiency experiments, the comparative role of each treatment in these experiments is noted in parentheses):

Treatment 0–Unfed control, filtered seawater
Treatment 1–T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2–T-ISO at 500 cells/μl (T-ISO bloom equivalent)
Treatment 3–M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4–M-POLY at 2000 cells/μl (bloom)

M-POLY, cultured to 3–6 × 10^3 cells/μl, was centrifuged and resuspended in filtered seawater to give an algal cell concentration on the order of 1 × 10^5 cells/μl for the preparation of treatments 3 and 4. Each diet was fed to three replicate (2 larvae/ml in 1500 ml of seawater in 21 vessels). Larval cultures were sampled at the beginning of the experiment and at least after every water exchange (every 48 hr.) by slowly thrusting a perforated, acrylic plunger vertically downward seven times through the water column of each culture to suspend the larvae uniformity. Using a graduated plastic syringe (minimum diameter 3 mm), a 30 ml sample of culture water and larvae was removed immediately and placed in a sample tube containing ~2 ml of 30% buffered formalin (final concentration of formalin was ~2%). Larvae were counted and sized to the nearest 6 μm with a dissecting microscope (Wild model M3a) and ocular micrometer.

Larvae used in these experiments varied in age, shell length and feeding history at the beginning of the experiment (Table 2).

An instantaneous growth coefficient (k) was calculated for each larva using the following equation (e.g., Walne 1963, Bayne 1965, Malouf and Breese 1977):

$$k = \frac{\ln(\text{final individual length}) - \ln(\text{initial mean length})}{\text{elapsed time}} \times 100\%$$

Proportional data were arcsine transformed prior to statistical analysis (Zar 1984). Most statistical procedures were conducted using the subprograms of SPSSx on an IBM 3083 computing system. Homoscedastic data sets were analyzed with parametric one-factor and two-factor analyses of variance (ANOVA) and Student-Newman-Keuls (SNK) multiple range tests. Data sets with heterogeneous variances were analyzed with nonparametric Kruskal-Wallis one-factor and two-factor ANOVA as well as with nonparametric multiple comparison tests following the methods of Zar (1984).

TABLE 2.

Larvae used in growth and survival experiments.

Experiment	Age (hr.)	Shell length (μm)	Feeding history
1	52	103	unfed
2	54	94	unfed
3	121	100	unfed for 27 hr. then 50 T-ISO cells/μl for 95 hr.
4	153	117	unfed for 24 hr. then 50 T-ISO cells/μl for 129 hr.

Mortality

An instantaneous coefficient of mortality (Z) was calculated with the following formula:

$$Z = \frac{\ln(\text{initial number of larvae}) - \ln(\text{final number of larvae})}{\text{elapsed time}}$$

Parametric one-factor ANOVA were conducted for mortality coefficients for each experiment. The mortality here is actually a combination of mortality caused by the experimental treatments (experimental mortality) and "sampling mortality". Sampling mortality resulted from repeated sampling of small percentages (2%) of the total volume of a culture of larvae a number of times over the course of an experiment. No compensation for this loss of larvae was attempted.

RESULTS

Grazing Rate Experiments

Figure 2 presents age-specific grazing rates of larvae and postlarvae feeding on each species of algae. One cell of T-ISO was assigned an arbitrary value of one cell volume equivalent (CVE), therefore, based on cell diameter, one cell of M-POLY was equal to 0.25 CVE. Figure 3 presents age-specific grazing rates expressed as CVE/scallop/min.

Grazing rates of larvae peaked at nine days after fertilization and probably continued to increase before the onset of metamorphosis 11 days after fertilization. During the early stages of metamorphosis, grazing rates were negligible. At 13 days after fertilization, postlarval grazing rates on T-ISO were still nearly zero while M-POLY was being removed from suspension at much higher rates. From days 16–18, postlarvae were capturing similar volumes of both species of algae, however, by day 24, the CVE grazing rate for T-ISO was greater than that for M-POLY.

Absorption Efficiency Experiments

Figure 4 presents the results of the absorption efficiency experiments. In these experiments, larvae fed on four different diets of radiolabeled algae. Algal species rather than concentration differences affected the absorption efficiency of the scallop larvae. Larvae were able to absorb more carbon from T-ISO than from M-POLY regardless of cell concentrations. Cell concentration alone had no consistent effect on the absorption efficiency of the larvae (i.e., higher efficiencies on low concentrations in one experiment, lower efficiencies on high concentrations in the other).

An examination of counts of unabsorbed ^{14}C and ^{51}Cr in collected fecal material allows for a crude comparison of gut passage time for different diets. The data suggested that larvae feeding on low concentrations of T-ISO retained

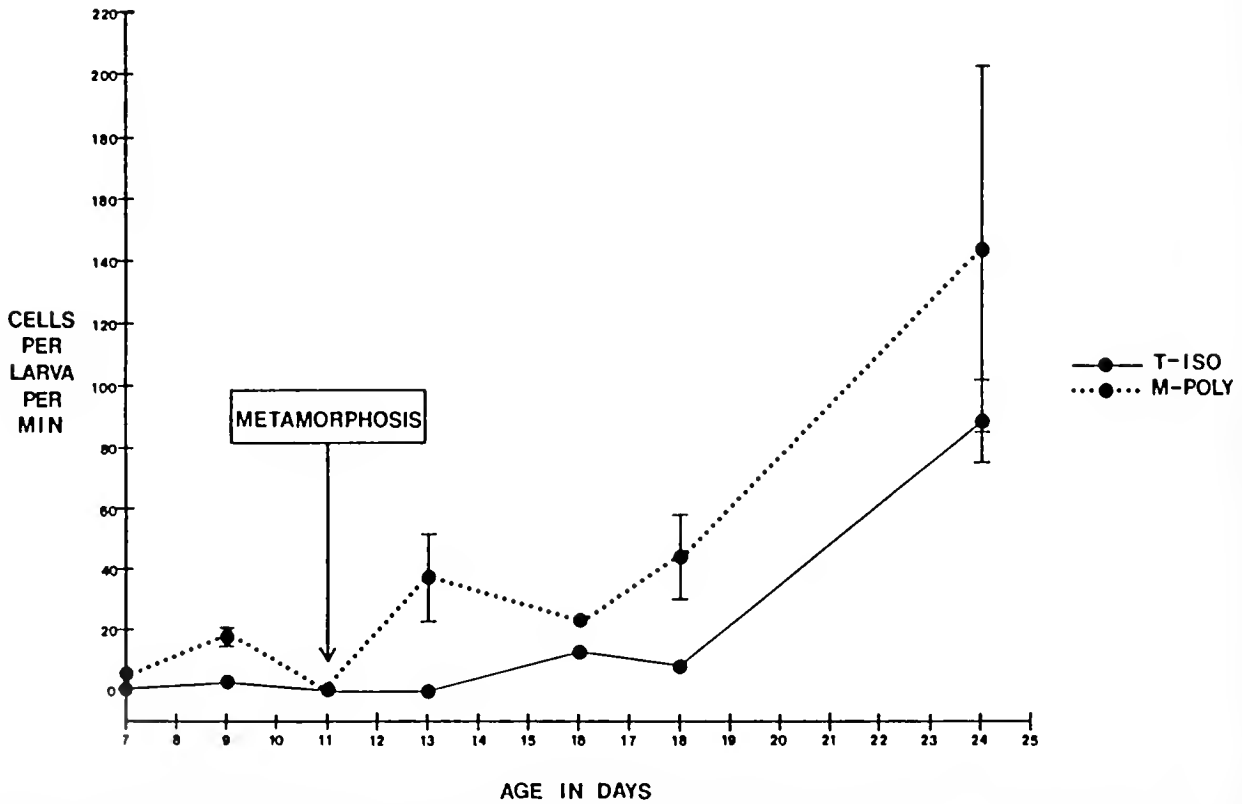

Figure 2. Grazing rates (cells/scallop/minute) of bay scallop veligers or juveniles at seven different ages (days after fertilization) feeding on two different microalgal diets. Error bars are ±S.E.

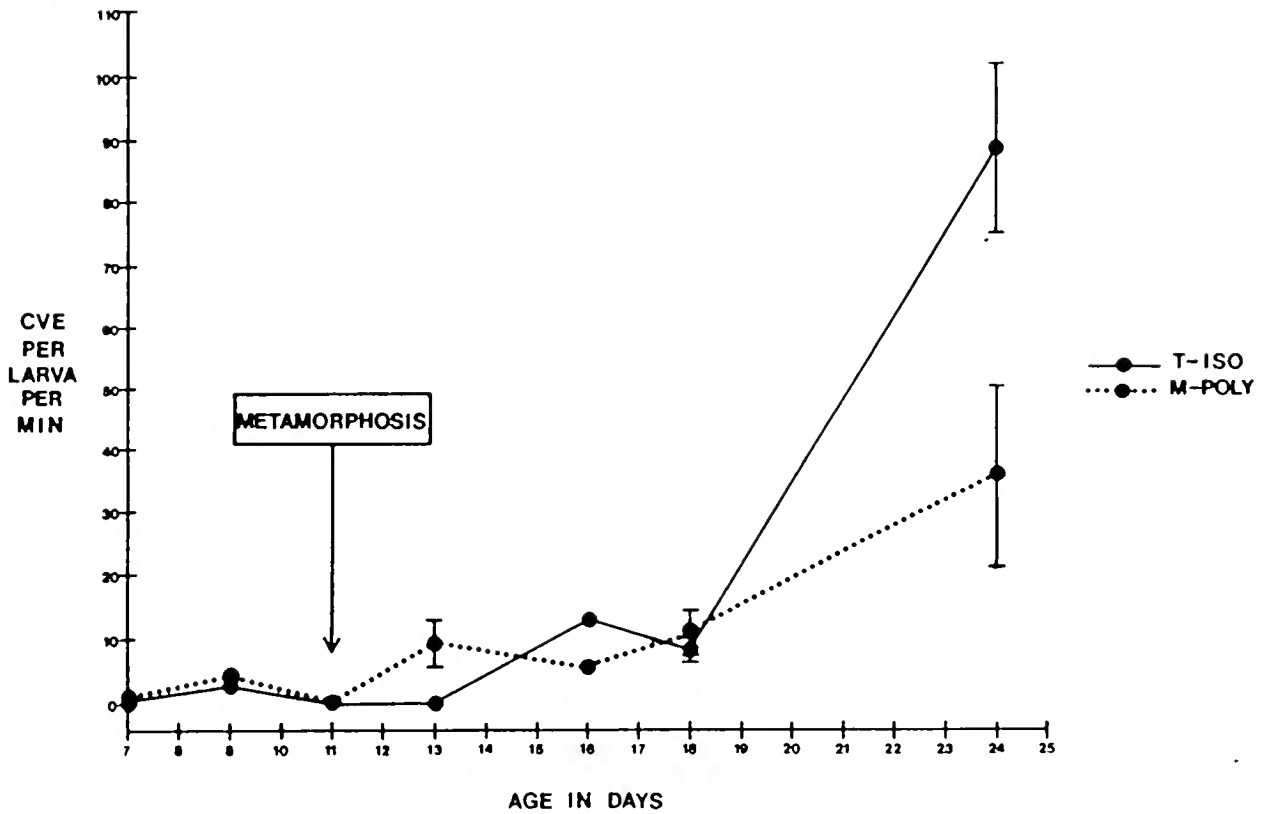

Figure 3. Grazing rates (CVEs/scallop/minute) of bay scallop veligers or juveniles at seven different ages (days after fertilization) feeding on two different microalgal diets. Error bars are ±S.E.

algae in their gut longer (mean of recovered fecal ^{14}C = 60.8% of total recovered) than did those larvae feeding on the higher concentration (85.9%). On the same basis, there was a smaller difference in gut retention time between treatments of M-POLY (mean of recovered fecal ^{14}C at the low concentration was 79.0% of total and 83.4% at the high concentration).

Growth and Survival Experiments

Table 3 illustrates differences in effects of treatments on larval growth coefficients. In experiments 1, 2, and 3, growth was affected significantly by algal species (at a = 0.05; parametric two factor ANOVA for experiment 1 and nonparametric Kruskal-Wallis two factor ANOVA for experiments 2 and 3). Generally, larvae fed T-ISO grew faster than larvae fed M-POLY. Statistically significant differences in the growth rates of larvae fed different concentrations of algae did exist, however, those differences were not consistent among any of the first three experiments.

In experiment 4, which used larger more fully developed larvae than the previous three experiments (see Table 2), concentration differences in the algal diets significantly affected growth rate ($p < 0.001$; two-factor parametric ANOVA) whereas effects of algal species were not significant ($p = 0.931$). In experiment 4, larvae fed the higher concentrations of T-ISO or M-POLY grew significantly more slowly ($p < 0.05$; one factor ANOVA and SNK multiple comparisons) than did larvae fed lower concentrations of either species of algae.

In experiment 1, neither algal species nor cell concentration significantly affected growth rates yet there was a significant interaction ($p = 0.049$) between these two factors. A nonparametric, one-tailed multiple comparison (Zar 1984) was conducted to determine if growth rates in the control diet (50 T-ISO cells/μl were greater than those observed in the other treatments. Multiple comparison tests with one-tailed hypotheses allow the detection of a statistically significant difference in only one direction (greater or less than), however, it employs a less conservative critical value for the test statistic Q (Zar 1984). In this analysis, larvae fed the low concentration of T-ISO were found to have grown significantly faster those fed the low concentration of M-POLY ($0.025 < p < 0.05$).

One factor ANOVA revealed no statistically significant difference in survival among treatments for all four experiments (p ranging from 0.121–0.438).

DISCUSSION

Cell Capture by Veligers

The results of the current study do not suggest that M-POLY was too small for scallop larvae to capture, further

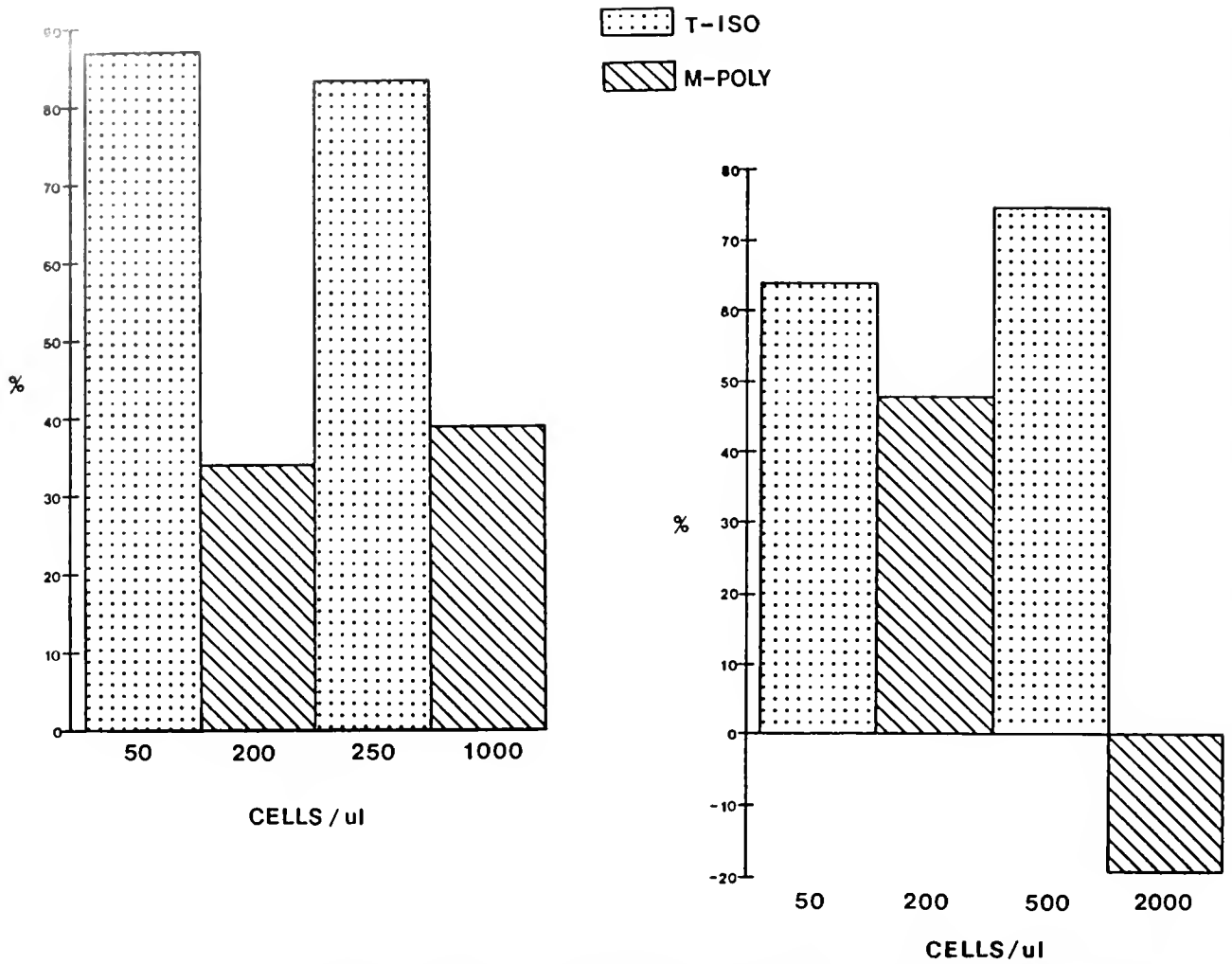

Figure 4. Absorption efficiencies (%) of scallop larvae feeding on different microalgal diets (absorption efficiency experiments 1 and 2).

suggesting that cell size alone was not a factor affecting the growth rate of scallop larvae fed this bloom isolate. In relative terms, the two algae were captured with similar efficiencies. M-POLY cells, which were provided at 4× the concentration of T-ISO cells, were captured by larvae at ~6–12 times the rate of T-ISO cells.

Based on the size of the algal cells, however, this result is not unexpected. Sprung (1984a) reported that *Mytilus*

TABLE 3.

Growth coefficients (k) calculated for bay scallop larvae fed five different diets in experiments 1, 2 and 3.

		Experimental treatment, mean k, (standard deviation)				
Experiment	**N**	**Unfed**	**M-POLY @ 200**	**M-POLY @ 2000**	**T-ISO @ 500**	**T-ISO @ 50**
1	207	0.045	0.107	0.151	0.159	0.175
		(0.048)	(0.083)	(0.079)	(0.096)	(0.110)
		Unfed	**M-POLY @ 2000**	**M-POLY @ 200**	**T-ISO @ 50**	**T-ISO @ 500**
2	158	0.009	0.713	0.095	0.132	0.197
		(0.045)	(0.035)	(0.057)	(0.075)	(0.069)
		M-POLY @ 2000	**Unfed**	**M-POLY @ 200**	**T-ISO @ 50**	**T-ISO @ 500**
3	452	0.200	0.024	0.036	0.079	0.093
		(0.063)	(0.057)	(0.055)	(0.082)	(0.107)

edulis larvae, when fed a wide range of particle sizes, were able to capture 3.5 μm (equivalent spherical diameter) particles with the greatest efficiency. Walne (1965) reported that *Ostrea edulis* larvae efficiently captured algae 3–10 μm in diameter. Wilson (1979, 1980) reported that *O. edulis* larvae were best able to capture algal cells 3–3.5 μm in diameter. Riisgard et al. (1980) reported an optimum size of 2.5–3.5 μm particles for *M. edulis* larvae. Thus, M-POLY (2.5–3.5 μm in diameter) is within a size range for efficient capture by bivalve larvae.

Cell Capture by Postlarvae

Palmer and Williams (1980) reported that the adult pectinid gill has a greatly reduced capture efficiency for particles less than 6–7 μm in diameter. In the current study, postlarvae (12 days after settlement) feeding on T-ISO captured more than twice the number of cell volume equivalents (CVE) per hour than did postlarvae of the same age feeding on M-POLY (Figure 3). This suggested a decrease in the relative efficiency with which the postlarvae were able to capture M-POLY. This result further suggested that the gill of *A. irradians* is functionally complete 12 days after settlement and metamorphosis, or has acquired the particle size-dependent filtration efficiencies characteristic of the adult gill.

Absorption and Growth

The dual-tracer method estimates absorption efficiency as the percentage of carbon ingested which is not egested. This method provides a number of advantages over indirect estimates of absorption efficiency or other radiotracer methods. Most importantly, the accuracy of this method does not depend on knowledge of ingestion rate. In other methods, ingestion rate is often equated with grazing rate, an assumption which is valid only when pseudofecal production is absent (Gallager and Mann 1980). However, as applied in the current study, several sources of error were present in this method, including errors resulting from bacterial respiration, excretion of unabsorbed ^{14}C without proportionate losses of ^{51}Cr, dissolution of feces and algal respiration after food samples were taken. Also, given the fact that ^{14}C moves through the larval gut at a much slower rate than ^{51}Cr failure to allow sufficient time for complete gut evacuation results in an overestimation of absorption efficiency. This last source of error may have been important in these experiments. A preliminary absorption efficiency experiment was conducted to estimate the length of time necessary for the larval gut to release the majority of the unabsorbed ^{14}C and ^{51}Cr, however, only dual-labeled M-POLY was available for this experiment. Estimates of gut retention time indicated that M-POLY was held in the gut for a shorter period of time than T-ISO. Thus the length of time for most of the undigested ^{14}C to be voided from the gut may have been an underestimation of the amount of time needed for most of the unabsorbed ^{14}C from T-ISO to be voided. Consequently, the absorption efficiency of scallop larvae fed T-ISO may have been overestimated by an unknown amount.

Absorption efficiencies were correlated to gut retention times for the two species of microalgae, suggesting that the comparatively greater absorption efficiencies measured for T-ISO are valid results and not artifacts due to incomplete recovery of undigested carbon. Bricelj et al. (1984) found that gut retention time paralleled absorption efficiency in juvenile hard clams (*Mercenaria mercenaria*). Clams experienced a much shorter gut retention time and lower absorption efficiencies when fed the small forms *Stichococcus* and *Nannochloris* than when they were fed *Pseudoisochrysis paradoxa*. Similarly, Pechenik and Fisher (1979) found that assimilation efficiency was correlated with the gut retention time. Indirect estimates of assimilation efficiency at algal cell concentrations similar to the "bloom-like" concentrations used in this study indicated efficiencies of approximately 28% (at 1000 cells/μl; Crisp et al. 1985). Sprung (1984c) estimated assimilation efficiencies of 85.8 and 61.6% at 2 and 40 cells/μl respectively with 150 μm *M. edulis* larvae, results which are comparable to those of our study at low algal cell concentrations. Overestimation of ingestion by ignoring pseudofecal production at high algal cell concentrations may explain the disparity between these indirect estimates and the direct measurements reported in this study.

Effect of Algal Species

Bay scallop larvae were not able to absorb carbon from M-POLY and T-ISO with equivalent efficiencies. Larvae were able to absorb a greater percentage of carbon from T-ISO than from M-POLY (higher growth on T-ISO in growth experiments 1, 2 and 3). Interspecific structural variations such as the presence or absence of a cell wall may explain why one species of algae is absorbed or assimilated more efficiently than another (e.g., Davis and Guillard, 1958, working with *Chlorella*). Similar to the cell wall of *Chlorella*, the organic sheath seen in electron micrographs of M-POLY cells may reduce the availability of algal cell contents for absorption. As noted earlier, this organic sheath was extremely refractory.

Effect of Concentration

Concentration-dependent absorption efficiency was not observed in the absorption efficiency experiments nor were there any consistent effects of concentration on growth rate in the first three growth experiments. From the literature it is unclear how bivalve larvae respond to concentrations of algae such as those seen in the 1985 phytoplankton bloom.

Based on Yonge's (1926) description of the physiology of larval bivalve feeding, Walne (1965) postulated that larvae have two external mechanisms for dealing with an overabundance of food. The larvae must either reduce the rate at which they are capturing particles or increase their

rate of pseudofecal production. An internal mechanism for responding to an overabundance of food could be a decrease in absorption efficiency, however, Walne (1965) found that although total assimilation increased as cell concentration increased, even up to very high concentrations (1000 cells/μl), the assimilation efficiency was relatively constant over a wide range of cell concentrations. Walne (1965) also found that the volume swept free of algal cells per larva (filtration rate) decreased as algal cell concentration increased over a range of 30–371 cells/μl. Since a reduction in assimilation efficiency was not observed as food concentrations increased, Walne (1965) concluded that larvae respond to increased food concentrations either by decreasing feeding activity or by decreasing filtering efficiency (increase pseudofecal production). Either response would maintain a constant rate of ingestion. In concurrence with Walne's (1965) results, Gerdes (1983) found that *Crassostrea gigas* larvae reacted to higher concentrations of food particles by lowering filtration rate to allow ingestion to remain constant at high and low food particle concentrations. Consequently, assimilation also remains relatively constant over a wide range of algal cell concentrations (Gerdes 1983).

In general, growth rates increase with increasing levels of food concentration up to a maximum growth rate at which additional increases in food concentration will not cause further increases in growth rate, yet results are equivocal. Some studies have found that growth rates remain relatively constant at optimal or supraoptimal food concentrations (Davis and Guillard 1958, Newkirk and Waugh 1980, Walne 1965, 1966). Reductions in larval growth rates at high algal concentrations have also been observed. Malouf and Breese (1977) reported reduced growth rates of *Crassostrea gigas* larvae at food concentrations higher than 20–40 cells/μl. (in agreement with Loosanoff et al. 1953, 1954, Rhodes and Landers 1973). Some investigators have suggested that high numbers of food particles alone can affect digestive processes of larvae and result in low growth at high algal cell concentrations. From observations of food movement through the gut of larval *Ostrea edulis*, Millar (1955) reported that there seemed to be no sorting mechanism in the larval gut. He stated that,

> "It is a matter of chance whether material drawn off into the midgut and thence passed to the rectum has been in the stomach for a short or a long time, and therefore to what extent it has been subjected to digestion" (Millar 1955).

Malouf and Breese (1977) cited Millar's (1955) observations as physiological evidence to explain the reduced larval growth rate often recorded at high algal cell concentrations. They hypothesized that a high concentration of food may cause larvae to pass some food particles through their gut relatively undigested. In this way larvae theoretically could eat themselves to death by feeding at a rate which surpassed their ability to digest the material. Energy would be expended toward capturing and ingesting the particles without proportionate energy gain through the digestion and assimilation of nutrients from the particle. Malouf and Breese (1977) also suggested excessive pseudofecal production as another important cause of reduced growth at high algal densities. In addition to the loss of energy through excessive mucus production, larvae may become entrapped in long strands of pseudofecal mucus (Malouf and Breese 1977, R. E. Malouf pers. comm.).

Others have suggested that toxic metabolites associated with high concentrations of algae may cause reduced growth. Toxic metabolites could accumulate (Loosanoff et al. 1954) or be produced as a function of the physiological state of the algal cells (Wilson 1979). The results of the grazing rate experiments suggest that M-POLY does not have associated with it extracellular metabolites which inhibit larval grazing rates as has been reported for other species (Loosanoff et al. 1954, Guillard 1958). We observed no reduction in growth rates of larvae fed the high concentrations of either species of microalgae in experiments 1, 2 and 3. It is possible that the culture vessels provided an environment in which microalgae maintained high rates of photosynthesis and reproduction thereby reducing some negative effects of high algal cell concentrations on larval growth.

There was significant growth rate depression at the higher algal cell concentrations in growth experiment 4, a result which runs counter to those of the other experiments. The reasons for this are not clear, however, a number of investigators who have worked with bivalve larvae (e.g., Malouf and Breese 1977, Babinchak and Ukeles 1979) were unable to explain poor correlation of growth among cultures treated similarly. Larvae of experiment 4 were older than larvae used in the previous three experiments and they reached a more advanced stage of development than did larvae of the other experiments. Several investigators have reported age-specific changes in the ability of bivalve larvae to utilize certain algal species as food.

Survival

The experimental treatments affected larval growth but not survival, however had the experiments been carried through metamorphosis, a critical period during which lipid reserves accumulated through planktotrophy maintain the non-feeding larvae (e.g., Gerdes 1983), it is likely that dietary effects on survival would have been observed.

CONCLUSIONS

The results of these laboratory experiments suggest that one algal isolate of the 1985 picoplankton blooms in the coastal embayments of Long Island cannot support adequate growth of bay scallop larvae. In light of the reproductive strategy (mature quickly and spawn only once) and early life history (planktotrophic larvae) of *Argopecten irradians*, this effect on larval growth was probably the most important impact, both ecological and economic, of the so-

called "brown tide" blooms. The resultant widespread failure of larval recruitment virtually eliminated the bay scallop fishery in New York.

While *Minutocellus polymorphus* is present in these persistent blooms, it is not the dominant phytoplankter; Sieburth et al. (in press) describe a new genus and species, *Aureococcus anophagefferens,* which dominates these widespread and recurring coastal phenomena. Our experimental results with *M. polymorphus* (which is very similar in size to *A. anophageferrens*) suggest that bay scallop larvae can capture such small food particles, but that as larvae complete metamorphosis and begin to feed as juveniles, particle size-dependence becomes apparent and ingestion rates on such small particles decline. Our results suggest that there is no effect of particle concentration on bay scallop veligers. Our absorption efficiency results infer that larval ingestion rates are nearly constant at both bloom and "optimal" particle concentrations. Lower growth was observed in late larvae and postlarvae feeding on high concentrations of *M. polymorphus* and the Tahitian strain of *Isochrysis* sp. Species differences between *M. polymorphus* and Tahitian *Isochrysis* were apparent in the larval growth study; carbon was absorbed less efficiently from *M. polymorphus* than from Tahitian *Isochrysis*. The essential nutritional composition of this bloom isolate remains unknown, however our results suggest that a qualitative aspect of the *M. polymorphus* diet (possibly reduced availability of cell contents of absorption) resulted in poor larval growth and settlement success for bay scallops spawning during recent picoplankton blooms in New York's coastal bays.

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POTENTIAL HAZARDS OF *DINOPHYSIS* TO CONSUMERS AND SHELLFISHERIES

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ABSTRACT Diarrhetic (or Diarrheic) Shellfish Poisoning (DSP) is a newly identified global public health risk which also threatens the full utilization of valuable shellfish resources. Human gastrointestinal illness results from ingestion of bivalves which have fed upon toxic species of the planktonic dinoflagellate genus *Dinophysis*. It is only in the last decade that the symptoms, toxins, and etiologic agents were identified. Numerous epidemiologic and environmental factors complicate diagnosis, monitoring efforts, and closure decisions of shellfish growing waters. Due to the recent recongition of DSP, many past shellfish-related incidents may have been wrongly attributed to bacteria, viruses, or unknown causes. Worldwide retrospective epidemiologic investigation has identified incidents which can now be reclassified as "probable DSP", based on symptoms as well as temporal and spatial distribution of *Dinophysis*. Plankton monitoring in Nassau County, Long Island, waters recovered twelve species of *Dinophysis*, often several together. *D. acuminata*, *D. norvegica*, and *D. acuta* were most prevalent. Management needs include laboratory and field studies, education, monitoring, and closure protocol.

KEY WORDS: Diarrhetic Shellfish Poisoning (DSP), *Dinophysis*, toxic dinoflagellate, shellfish-related illness, plankton monitoring

INTRODUCTION

Diarrhetic (or Diarrheic) Shellfish Poisoning (DSP) has been formally known to the scientific and medical communities for only a decade. The classic Japanese work described the symptoms (Yasumoto et al. 1978), gave a descriptive name to the syndrome (Yasumoto et al. 1980), identified the fat-soluble toxin, dinophysistoxin-1, a methyl-okadaic acid (Yasumoto et al. 1979, Murata et al. 1982), and identified the dinoflagellate etiologic agent, *Dinophysis fortii* Pavillard) (Yasumoto et al. 1980). Japan initiated monitoring for DSP in 1978 when illnesses from 1976 and 1977 were traced to DSP from scallops and mussels (Yasumoto et al. 1980).

Several other species of the genus *Dinophysis* have since been directly or indirectly associated with DSP, including *D. acuminata* (Claparéde and Lachmann) *D. acuta* (Ehrenberg), and *D. norvegica* (Claparéde and Lachmann) (Steidinger and Tangen 1985). Additional toxins have been identified and cases documented worldwide (Murata et al. 1987, Yasumoto 1987). Many countries, including Ireland, France, Norway, Sweden, the Netherlands, and Spain in Western Europe; the United States, Canada, and Chile in the Americas; Japan, Thailand, and New Zealand on the Pacific; and India, are conducting scientific studies and/or monitoring, mainly in response to DSP illness episodes. DSP is now recognized as both a global public health risk and a threat to the full utilization of valuable shellfish resources.

DSP SYNDROME

Human gastrointestinal illness results from the ingestion of shellfish which have filter-fed upon one or more toxic species of the planktonic genus *Dinophysis*. Normal cooking does not destroy the toxins (Yasumoto et al. 1978). A minimum of only twelve mouse units (M.U.) of dinophysistoxin-1 or okadaic acid causes human illness (Yasumoto et al. 1980). A mouse unit is the smallest amount of extract that will kill a 20 g mouse in 24 hr., and corresponds to 3.2 ug of dinophysistoxin-1 or 4.0 ug of okadaic acid.

The main symptom of the disease is reflected in its name. In addition to the mild to severe diarrhea, most patients suffer nausea and vomiting, and moderate to severe abdominal pain and cramps, possibly accompanied by chills. Typical cases show initiation between three to seven hours after ingestion. Symptoms, however, can begin as early as 30 min., or as late as 10–15 hr., but seldom exceed 12 hr. No diagnostic medium, such as blood, urine, saliva, or stool, can currently be tested for the toxins.

No known fatalities have been recorded and total recovery usually occurs by the third day, even without medical assistance. Some people who developed fluid and electrolyte imbalance as a result of prolonged symptoms required medical aid. No lingering or later distress has been recorded. Exposure does not provide immunity. Although DSP is caused by potent toxins, there appears to be distinct human variation to toxin susceptibility (Underdal et al. 1985). The tumor promoting activity reported for okadaic acid and dinophysistoxin-1 (Fujiki et al. 1987, Suganuma et al. 1988) calls for attention to potential risks of taking these toxins, even at low doses.

MANAGEMENT CONSIDERATIONS

A number of epidemiological and environmental factors complicate DSP management. As information spreads and publicity about DSP increases, more areas report current and past DSP episodes, prompting studies and adding to the number of species reported to be toxic. When more than one *Dinophysis* species is present, pinpointing the source of toxicity is more difficult. Also, an area may have DSP even

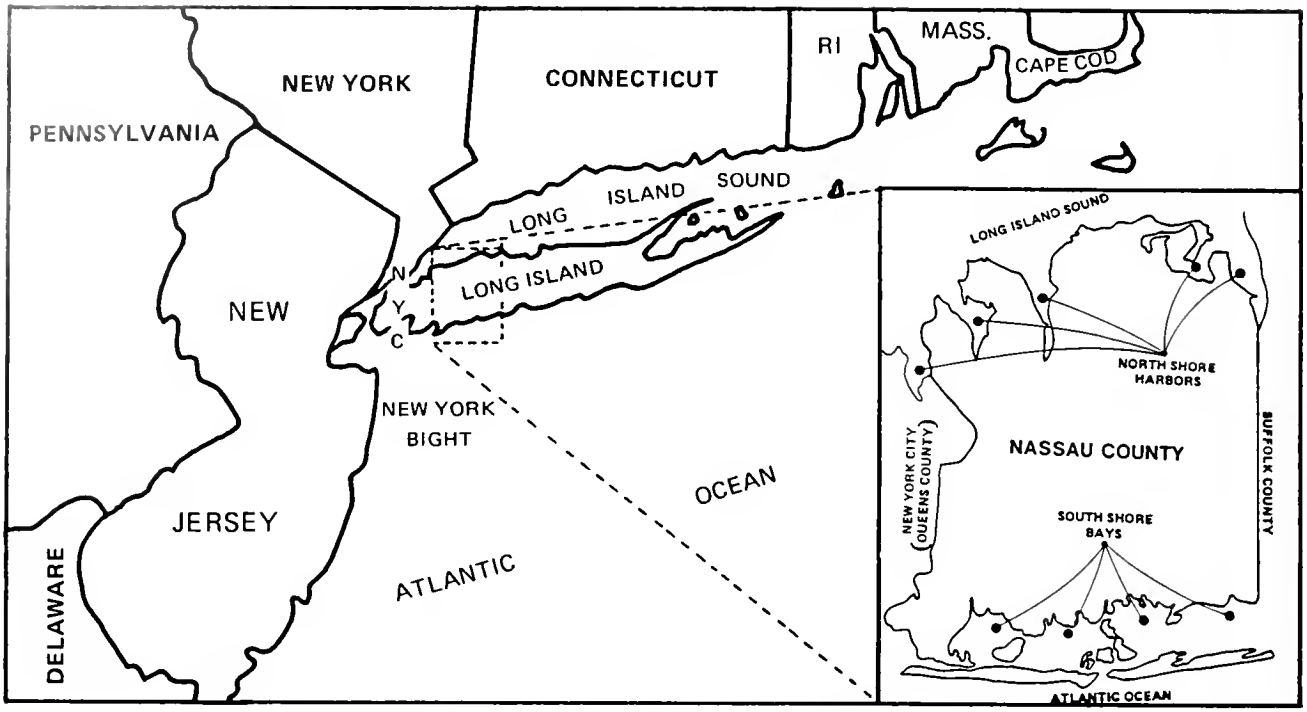

Figure 1. Nassau County, New York vicinity map.

with very low numbers of *Dinophysis,* compared to other species (Dahl and Yndestad 1985). Shellfish toxicity has been rather short-lived in most European waters and in Japan (Underdal et al. 1985), but a distressing prospect for the industry comes from more northern waters. In some areas such as Norway and Sweden, the shellfish toxicity lasted long after the bloom of *Dinophysis* ended, possibly due to lower shellfish metabolic rate in cold water, preventing or delaying detoxification (Krogh et al. 1985).

Diagnosis has been further complicated because the implicated toxins and dinoflagellates significantly differ between Japan and other countries (Yasumoto 1985). In many European episodes, *D. acuminata* is thought to be the main toxin source (Lassus et al. 1985). Recently, in waters just north of Long Island, Maranda and Shimizu (1987) confirmed the toxicity of this species in Narragansett Bay, Rhode Island (Figure 1). However, toxicity of specific *Dinophysis* species varies spatially and temporally, and the number of cells per liter which will precipitate toxicity can also vary. For example, counts of *D. acuminata* more than 200 cells/liter correlated with shellfish toxin levels in French coastal waters (Marcaillou-LeBaut 1985), but only blooms greater than 20,000 cells/liter were followed by diarrhetic mussel poisoning in the Dutch Waddensea (Kat 1983).

In some geographic areas, including parts of the northeast United States, suspect toxic *Dinophysis* species appear concurrently with another toxic dinoflagellate, *Protogonyaulax tamarensis* ((Lebour emend. Taylor) Taylor), the causative agent of Paralytic Shellfish Poisoning (PSP). This combination of toxins adds to the severity and range of symptoms in the patient and complicates diagnosis. In the first reported episode of this type, all three victims exhibited the gastrointestinal symptoms of DSP as well as the neuromuscular effects associated with PSP (Freudenthal and Jijina 1985). On one occasion in southwest New Brunswick, Canada, a probable DSP syndrome was complicated by the low-level presence of the PSP species in the shellfish (Richard pers. comm.).

This co-occurrence of toxic genera also complicates monitoring efforts and closure decisions related to shellfish growing waters. An agency performing PSP toxin mouse assay would not normally detect DSP toxins. New problems with this double presence have been recognized in areas with long established PSP monitoring programs such as Maine (Hurst pers. comm.) and neighboring New Brunswick (Richard pers. comm.).

Another puzzling factor is that while ecological data show abundant *Dinophysis* populations worldwide, there have been relatively few illness episodes reported and confirmed, and these episodes varied widely from several thousand to only a few victims (Yasumoto 1987). A partial explanation is the varying toxicity of *Dinophysis* populations. Underreporting of mild cases and/or misdiagnosis of reported gastroenteritis cases is another problem.

Many past shellfish-related gastrointestinal disorders have undoubtedly been wrongly attributed to "sewage", bacteria (Kat 1985), viruses, allergic reactions (Shimizu 1983) or unknown causes, due to the only recent recognition of DSP, the rather limited dissemination of informa-

tion among consumers, physicians, agencies, and industry; and the confusion in diagnosis. While other food-related gastrointestinal illnesses have similar symptoms, such as Norwalk virus, the times of onset and duration of symptoms are critical to the diagnosis of DSP.

With new awareness of the symptoms, timing, and causative agents, retrospective epidemiologic investigations worldwide are now reinspecting episodes that were probably incidents of DSP (Underdal et al. 1985), but were labeled "unidentified shellfish or mussel poisoning", such as the 1961 episode described by Kat (1979, 1985). In Venezuela, many diarrhetic cases after shellfish consumption had not previously been connected to the occurrence of dinoflagellates, although several *Dinophysis* species are known to be quite abundant (Reyes and Reyes pers. comm.). Anecdotal evidence suggests that DSP has been a problem in Atlantic Canada in the recent past (Wildish and Martin pers. comm.).

A recent search of "clam and shellfish-related illnesses" in the files from the last seven years of the Nassau County Health Department has recognized about a dozen one or two person isolated incidents which can now be reclassified as "probable" DSP. These designations are based upon symptoms and timing, negative results from conventional testing, as well as the seasonal and spatial distribution of *Dinophysis* from the monitoring data (Freudenthal 1982, 1983, 1985, 1986, unpublished reports). The cases were primarily from consumption of steamed mussels, *Mytilus edulis* (Linne); raw hard clams, *Mercenaria mercenaria* (Linne); and steamed soft-shelled clams, *Mya arenaria* (Linne).

In addition, several "undiagnosed" illnesses related to eating scallops presented typical DSP symptoms and timing. This is unexpected in our population; except for certain ethnic groups, scallop digestive tissue is not eaten. The lipid-soluble DSP toxins are known to accumulate in the hepatopancreas (digestive gland) of shellfish. While the hepatopancreas is ingested when the entire shellfish body is eaten, as with mussels, clams, and oysters, it is discarded when only the scallop adductor muscle is consumed.

This apparent occurrence of scallop-related DSP might result if the scallops were insufficiently washed, if scallop juices were used in cooking, or if incomplete cleaning left some digestive tissue attached to the muscle meat. Recent studies in Maine on the sea scallop *Placopectin megellanicus* (Gmelin) have found digestive tissues full of *Dinophysis* (Shumway 1987), and the scallops *Patinopecten yessoensis* and *Clamynippoensis akazara* (*Clamynippoenis sterrari akazara*) have contained DSP toxin in Japan (Yasumoto et al. 1978).

Oysters have not yet been implicated in epidemiologic investigations. They are suspect, however, in two past incidents affecting over 500 people in 1972 and 1984 in northern New Brunswick. Low levels of *D. acuminata* (and *Prorocentrum compressum* ((Bailey) Abé) have been identified throughout Atlantic Canada but specifically in the bay associated with these two DSP-like episodes (Wildish and Martin pers. comm.). Oysters have been found to be mildly toxic (Yasumoto et al. 1978). In some toxicological studies where mussels had significant toxin accumulations, oysters in the same area appeared nontoxic with negligible toxin accumulation. In France, for example, because of

TABLE 1.

Geographic distribution of *Dinophysis* species (1971–1986).

	Number of Sightings				
Species Name	North Shore Harbors (480 Samples)	Long Island Sound (34 Samples)	South Shore Bays (632 Samples)	Atlantic Ocean (146 Samples)	Total for All Areas (1292 Samples)
Dinophysis acuminata	125	14	121	91	351
Dinophysis acuta	1	0	17	12	30
Dinophysis caudata	0	0	2	2	4
Dinophysis fortii	0	0	8	19	27
Dinophysis lenticula	0	0	1	0	1
Dinophysis micropterygia	0	0	7	7	14
Dinophysis mitra	1	0	5	0	6
Dinophysis norvegica	2	1	32	26	61
Dinophysis ovum	1	0	4	4	9
Dinophysis rotundata	0	0	5	10	15
Dinophysis schroederi	0	0	1	2	3
Dinophysis tripos	1	1	9	14	25
Dinophysis sp.*	65	0	43	0	108
TOTAL SIGHTINGS	196	16	255	187	654

* These 108 sightings were identified only to genus.

DSP there have been bans on the harvesting and marketing of several species of clams and especially blue mussels, but rarely for oysters (Marcaillou-LeBaut 1985).

No reported DSP cases have involved gastropods. All shellfish found toxic have so far been bivalves (Ministry of Health and Welfare, Japan, 1981).

DINOPHYSIS IN NASSAU COUNTY WATERS

Long Island is surrounded by waters rich in assorted shellfish. There is a large consumer population , as well as a strong recreational and commercial shellfishery in the adjacent waters of the Atlantic Ocean, south shore bays, north shore harbors, and Long Island Sound (Figure 1). Approximately 1300 monitoring samples (surface tows or pumped integrated water samples) collected between 1971 and 1986 in Nassau County waters have been analyzed for distribution and abundance of phytoplankton and zooplankton. Another 200 samples from 1987 and 1988 await analysis.

Twelve species of *Dinophysis,* includign the species suspected of being toxic, have been identified. All twelve species have been observed in the south shore bays, ten in ocean samples, and six in north shore harbors. Sampling from the Sound has thus far been limited (Table 1).

D. fortii, the original Japanese toxic species, has been observed only in the ocean and the south shore bays. Three other incriminated or suspect species, *D. acuminata, D. norvegica,* and *D. acuta,* were observed in all areas, except *D. acuta* which was not recorded from Long Island Sound. These three species are the most common *Dinophysis* in the coastal waters of western Sweden (Edler and Lindahl 1987).

D. acuminata is by far the most prevalent species in all Nassau waters. In the north shore harbors, the other five species observed have only been recorded once or twice in these samples. In the south shore bays and ocean, the next most frequent species is *D. norvegica,* followed by *D. acuta.* Less common species are *D. fortii, D. tripos,* and

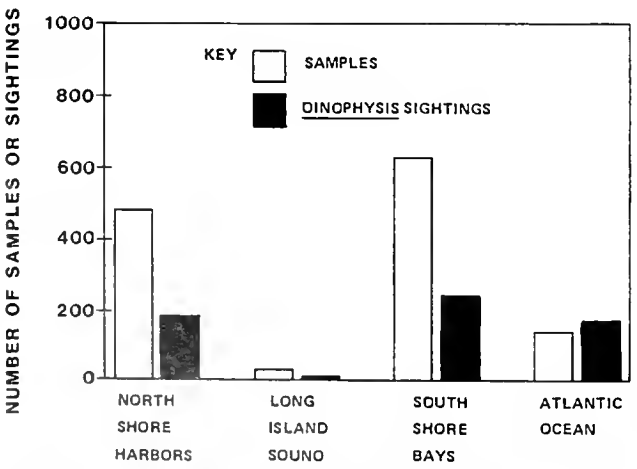

Figure 2. Geographic distribution of *Dinophysis* sightings 1971–1986.

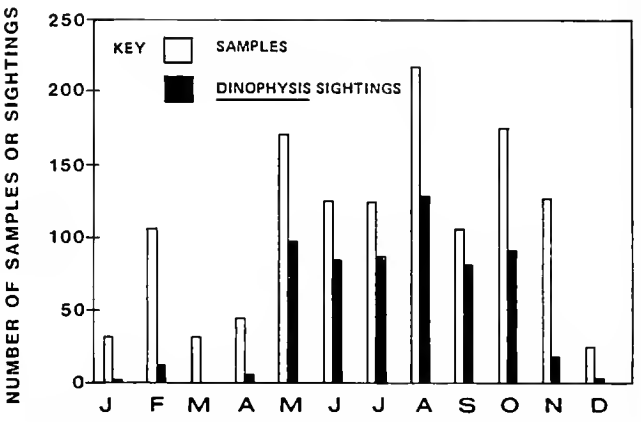

Figure 3. Seasonal distribution of *Dinophysis* sightings 1971–1986.

D. rotundata ((Claparéde and Lachmann) Abé). The remaining species were each recovered from 1–7× in each area (Table 1). Of these species, Yasumoto (1985) detected toxins in *D. tripos* and in samples containing *D. mitra* ((Schütt) Abé rel Balech) (Yasumoto 1985) and *D. caudata* has been blamed for mussel poisoning in Thailand (Sudara et al. 1984).

There have been 616 observations of *Dinophysis* species, often several species per sample. The ratio of samples to sightings is farily similar for the harbors, bays, and Sound, but the greatest frequency of sightings is in the ocean samples, with 175 sightings from 146 samples analyzed (Figure 2). *Dinophysis* was recovered in all months except March, with ninety-three percent of the sightings in May through October, our time of warmest waters (Figure 3).

For the 293 samples where cell counts were available, *Dinophysis* was signted 209 times. Of these, one half (104) were counts above 200 cells/liter, with 14% greater than 1000 cells/liter. The highest count from these samples was in July, 1984, at 13,000 cells/liter of *D. acuminata* in north shore Cold Spring Harbor. Counts as low as 200 cells per liter of *D. fortii* have been shown to cause DSP (Yasumoto et al. 1980).

The seasonal trend in *Dinophysis* occurrence was also evident in abundance. The highest counts (over 1000 cells/liter) made up 16% of the May sightings, 25% in June, peaked at 38% in July, declined to 12% in August, and were then rarely observed. By November, all observations were <200 cells/liter (Figure 4). Individual species showed seasonal variation as well. Counts greater than 200 cells/liter of *D. norvegica* and *D. acuta* were concentrated in May–July samples, while similar counts of *D. acuminata* spanned May to October, peaking in September.

Geographically, high counts (above 1000 cells/liter) were most prevalent in the north shore harbors (28% of sightings) and rarely observed at the stations in the south shore bays (6%) (Figure 5).

Results from an ocean sampling survey on July 1, 1988

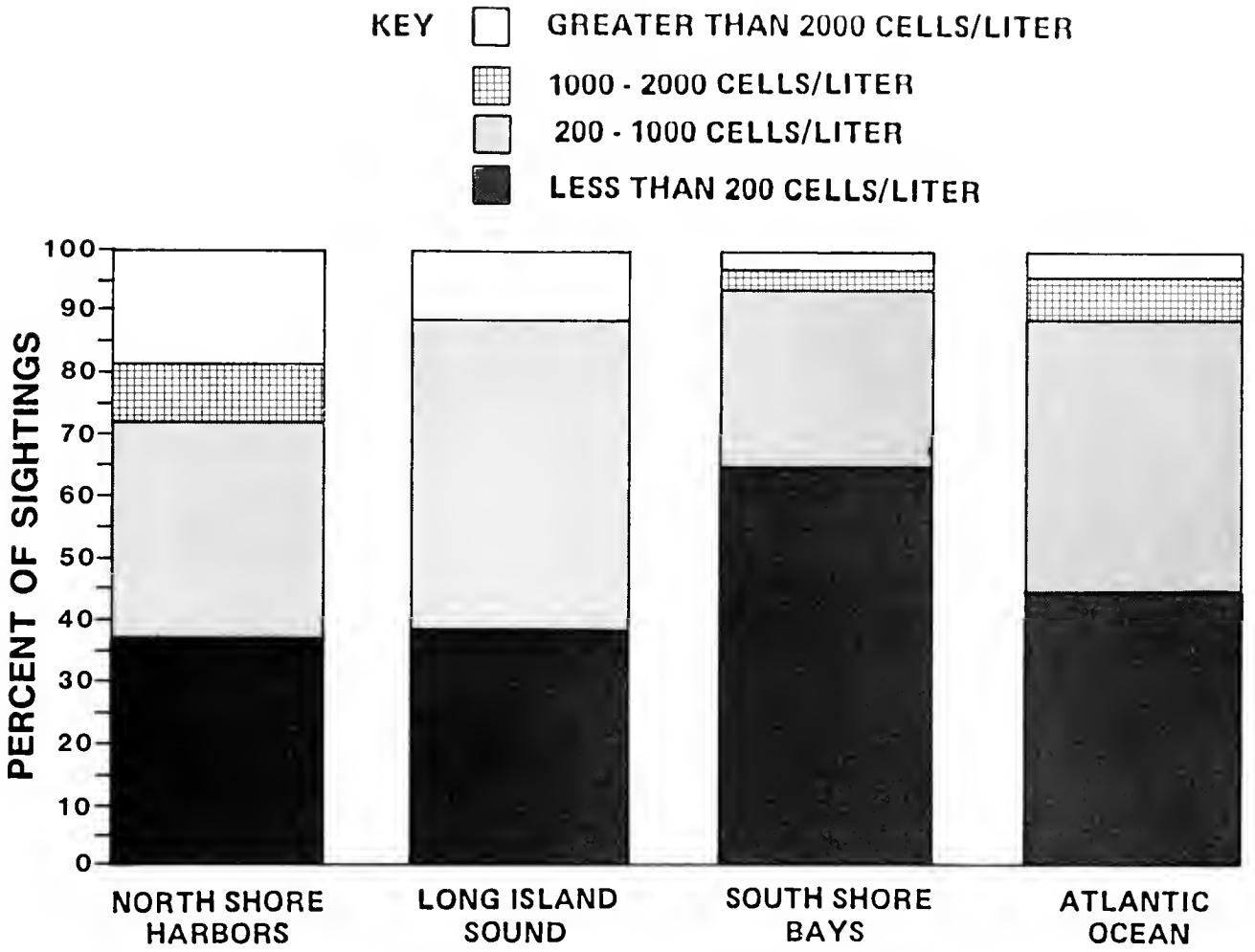

Figure 4. Cell densities of *Dinophysis* sightings by geographic area, 1984.

are incomplete, but 50,000 cells/liter of *D. acuta* were found at 15 m (the bottom of the thermocline) in waters five miles off the Long Island south shore coast. This is similar to recent findings by Edler and Lindahl (1987) off the western Swedish coast where *D. acuta* peaked at a depth of 10–20 m. On June 30, 1978, in New Jersey waters just south of Long Island (Figure 1) counts as high as 3,000,000 cells/liter of *Dinophysis* species (predominantly *D. acuta*, Olsen pers. comm.) were reported in a bottom sample taken one mile off Atlantic City (Figley 1978).

MANAGEMENT RECOMMENDATIONS

For resolution of this newly recognized global problem, several needs must be addressed. Culture of *Dinophysis* and ecological field work would permit the biology of the genus and environmental stimuli for blooms to be examined. This would identify environmental conditions which stimulate blooms, as well as pinpoint probable locations and seasons of abundance. However, *Dinophysis* culture has proven difficult. As emphasized five years ago by New Zealand researchers coping with suspected DSP in their green-ribbed mussel (*Perna canaliculus*) (Cassie pers. comm.), these data are essential for maximizing monitoring efforts and for predictive purposes.

To maintain the quality of the product and adequately protect the consumer, monitoring for toxicity (cell counts and/or shellfish assays) should be added to routine bacteriological testing at times and places where toxic dinoflagellates are known to occur, as established through routine reconnaissance. *Dinophysis* species do not distinguish between waters "open" (certified) and "closed" to shellfishing. Current work on assays such as the suckling mice (Hamano et al. 1985), high-performance liquid chromatography (HPLC) (Lee et al. 1987), or enzyme-linked immunosorbant assay (ELISA) which detects dinophysistoxin-1 and okadaic acid (Usagawa et al. pers. comm.), should lead to an international standard. Management plans similar to existing PSP procedures should be developed, as in France (Lassus et al. 1985) to outline closure due to DSP.

To upgrade the critical case history interview, diagnosis,

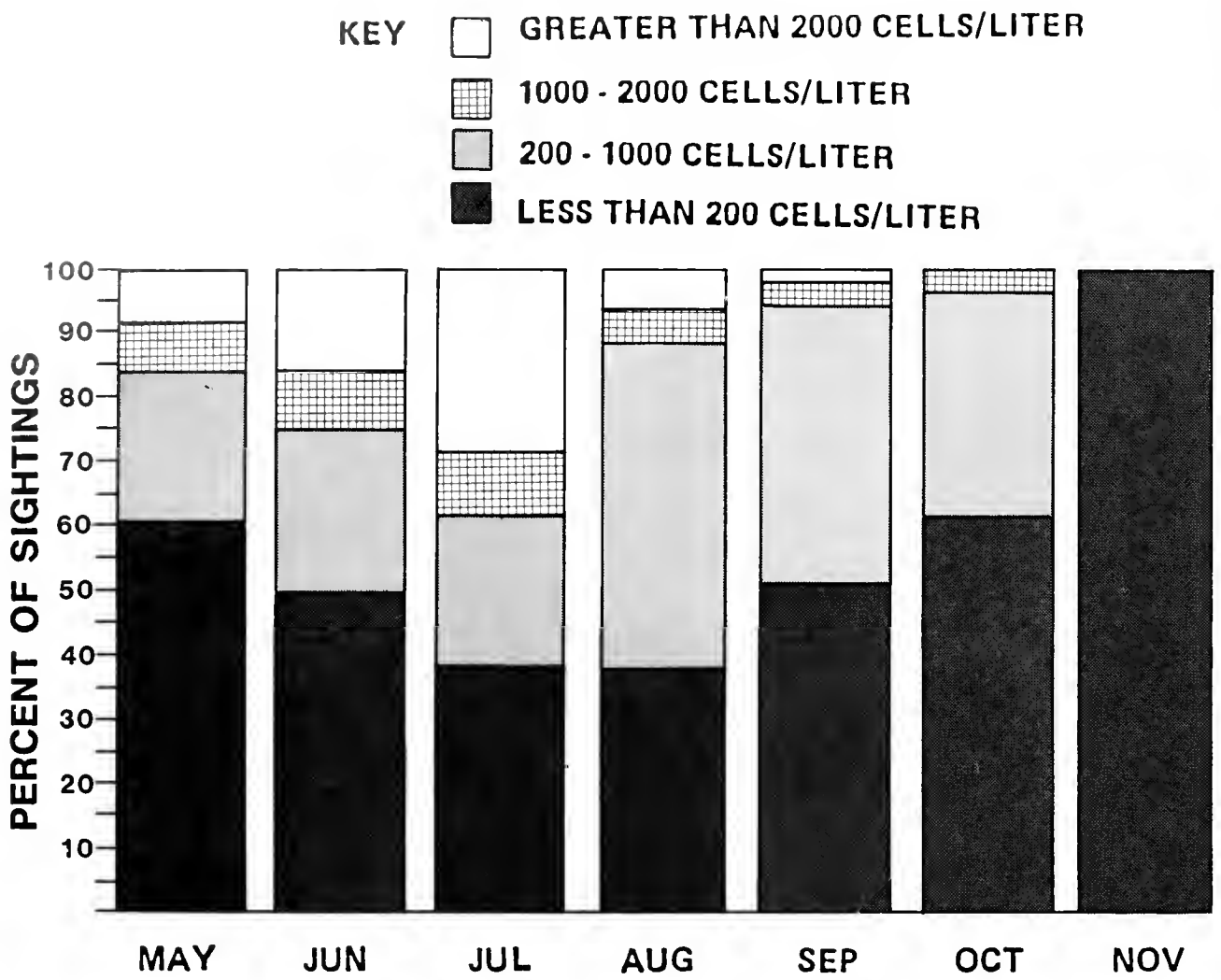

Figure 5. Cell densities of *Dinophysis* sightings by month, 1984.

treatment, and prompt reporting, the medical community, and especially hospital emergency rooms, must be brought up to date about shellfish-related diseases. Consumer education would also increase reporting of mild cases.

To facilitate illness investigations, communication must be enhanced between food protection agencies and their environmental counterparts. Foodbourne illness inspection and victim questionnaires should be expanded to include observations and questions relevant to toxic dinoflagellates. All cases of gastroenteritis with symptom onset time of less than 12 hr. should be investigated for DSP (Stamman et al. 1987). The remaining product from the tagged bushel is needed for both microscopic and toxicological examination. In addition, as soon as possible after the illness is reported, shellfish and water samples from the suspected growing site must be collected for toxin analysis and dinoflagellate species identification. Because the whole field of toxic dinoflagellates is advancing so rapidly and is so variable, it is imperative to save shellfish-related illness files indefinitely. These will be useful for retrospective studies which should be conducted now on all available files and again after new developments.

Effective management has substantially reduced the potential menace of PSP. Similar steps must now control the new global health problem of DSP and continue to insure the integrity of the world's shellfisheries. The causative genus appears to be cosmopolitan and to occur in potentially toxic levels on a regular basis. The ability to predict or recognize an episode as it occurs will prevent or minimize illness. Management plans must be developed which include as a minimum: education, monitoring for toxic species, and plans for closure of growing areas when necessary. These steps will help maintain consumer health and confidence as well as minimize economic effects.

ACKNOWLEDGMENTS

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OZONE DEPURATION OF BIVALVES CONTAINING PSP: PITFALLS AND POSSIBILITIES

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It is well-documented that certain bivalves concentrate toxic dinoflagellates in their tissues, making them vectors of paralytic shellfish poison (PSP) and thus toxic to vertebrates. Rates of toxin accumulation and elimination in and from bivalves differ with regard to species: *Mytilus edulis* rapidly accumulates and eliminates toxins from its tissues; *Spisula solidissima* concentrates PSP more slowly than *M. edulis* but can bind the toxins for months after a bloom dissipates; and *Mya arenaria* appears to fall between the other two species, both in toxin concentrations and elimination (Medcof et al. 1947).

Investigators have sought a technique that would permit the detoxification of PSP concurrent with the depuration of bacteria pathogenic to humans from affected bivalves.

In 1929, Violle reported that ozone, a triatomic form of oxygen and a powerful oxidant, was effective in sterilizing seawater. Presently, ozone is used routinely in France to disinfect seawater used in depuration stations (Fauvel 1963, Fauvel et al. 1979, Fauvel et al. 1982). In the 1970's, the above information spurred an investigation to determine the ability of ozonized seawater to inactivate PSP. This paper will present a brief review of the work to data on ozone detoxification of PSP, and then explore the pros and cons of the technique as perceived at present.

WORK TO DATE

In late 1972 and early 1973, investigators observed that ozone gas could inactivate *Gymnodinium breve* toxins in both laboratory grown cultures and field samples (Blogoslawski et al. 1973, Blogoslawski et al. 1975a). It was also determined that ozone gas could detoxify paralytic shellfish poisons from *Gonyaulax* spp. (Thurberg 1975). In the latter studies *G. catenella* toxin was obtained as a purified reference standard (saxitoxin) and *G. tamarensis* (*excavata*) toxin was extracted from toxic clams during a bloom that closed shellfish beds in Maine and New Hampshire. These toxins were rendered completely inactive, as measured by mouse bioassay (APHA 1970) after 5-min. doses of 2% ozone in air, flowing at a rate between 55 and 110 ml/min. Control situations were treated with compressed air to be certain that it was ozone, not the action of air bubbling through the solutions, that inactivated the toxins. All samples treated with air retained their original toxicity. The data obtained from these PSP studies are presented in full in a paper by Dawson et al. (1976) and are summarized in Table 1.

In August, 1974, the opportunity to test the efficacy of ozone to detoxify PSP in a field study was presented when a bloom of *Gonyaulax tamarensis* occurred in Gloucester, Mass., turning the seawater red and producing counts in the raw water up to 1.5×10^7 motile cells/liter. A continuous flow ozone-seawater contacting system was assembled and used to ozonize 864 l of toxic seawater a day. The water was directed to flow over non-toxified Milford-obtained clams (*Mya arenaria*) and mussels (*Mytilus edulis* and *Guekensia* (*Modiolus*) *demissus*) as well as similar toxified species from the Gloucester area. Equal numbers of control animals were set in similar trays which received 864 liters of untreated water per day (Figure 1). This laboratory experiment was conducted before, during, and after the peak of a PSP red tide bloom using seawater from the bloom area. No motile cells were found after ozonization, and approximately 60% of the ozonized dinoflagellates showed disrupted cell walls. Ozonized cells were characteristically larger than untreated controls, indicating possible damage to cell permeability.

After the *G. tamarensis* (*excavata*) counts subsided to about 3000 cells/l, samples of the clams and mussels were prepared for toxicity testing using the standard mouse bioassay. Bioassays to test extracts of clams (*Mya arenaria*) and mussels (*Mytilus edulis* and *Guekensia* (*Modiolus*) *demissus*) in ozonized red tide seawater indicated that ozone treatment does prevent shellfish from accumulating paralytic shellfish poison during red tide outbreaks. In non-ozonized seawater shellfish used for controls, held at the same time and flow rate, accumulated from 10–35× the amount of toxin necessary for closure of the shellfish beds (80 ug/100 g of meats). The field study ended on September 5, 1974, but additional tests at Milford were continued to confirm initial findings (Dawson et al. 1976).

In 1975, the efficacy of ozone in the detoxification of shellfish contaminated by red tide metabolites was again

[1]The use of trade names is merely to facilitate description and does not imply endorsement by the National Marine Fisheries Service or NOAA.

examined. After a bloom event of about 2 days' duration in Gloucester, MA, equipment was assembled to pass ozonized seawater across 10 trays which contained 60 surf clams, *S. solidissima*, 65 soft-shelled clams, *M. arenaria*, and 560 blue mussels, *M. edulis*. The control consisted of five additional trays which received untreated seawater containing 40 surf clams, 65 soft clams, and 210 blue mussels. The experiment was conducted for 3 days.

Using the standard mouse bioassay procedure, the following reductions in toxicity during the experimental period with ozonized seawater as opposed to control animals were obtained: *Mytilus edulis*, 30% reduction; *Spisula solidissima*, 31% reduction; and *Mya arenaria*, 0% reduction. *M. arenaria* were held in the ozonized water for only 14 working hours of the experiment, which apparently was too short a time for depuration or detoxification. In September 1975, a series of ozone detoxification experiments with red-tide contaminated surf clams (*S. solidissima*) was completed with a 17% reduction in toxicity over controls for a 96-hour depuration time. Results of the studies were published together (Blogoslawski and Stewart 1978).

In 1977, another attempt was made to use ozonized seawater to inactivate PSP-contaminated *Mya arenaria*. The study took place at Boothbay Harbor, Maine. Following 3 days of refrigeration, 360 healthy clams containing PSP (*M. arenaria* from New Brunswick, Canada) were evenly distributed among three racks, each containing five shallow fiberglass trays and supplied with 16°C seawater flowing at 2.5–3.0 liter/min. Two of the tray racks received ozonized seawater, while the third received oxygenated seawater and served as a control. For the first 72 hours, 20 clams were removed from each rack of trays; 10 for PSP extraction and measurement and 10 for bacteriological analysis. Toxin measurement was achieved using the standard mouse bioassay (American Public Health Association 1970).

At the conclusion of the study, 20 living clams from each tray rack were iced and transported to Milford, Connecticut. There, oxygen consumption studies were conducted to assess any physiological stress due to ozone treatment. Measurements were made over a 4-hr. period with a Gilson Differential Respirometer[1] at 26°C on excised gill tissues from clams that had been exposed to oxygenated (control) and ozonized (experimental) seawater for 72 or 96 hr. Two concentrations of residual ozone were used in this experiment—0.5 and 1.2 ppm.

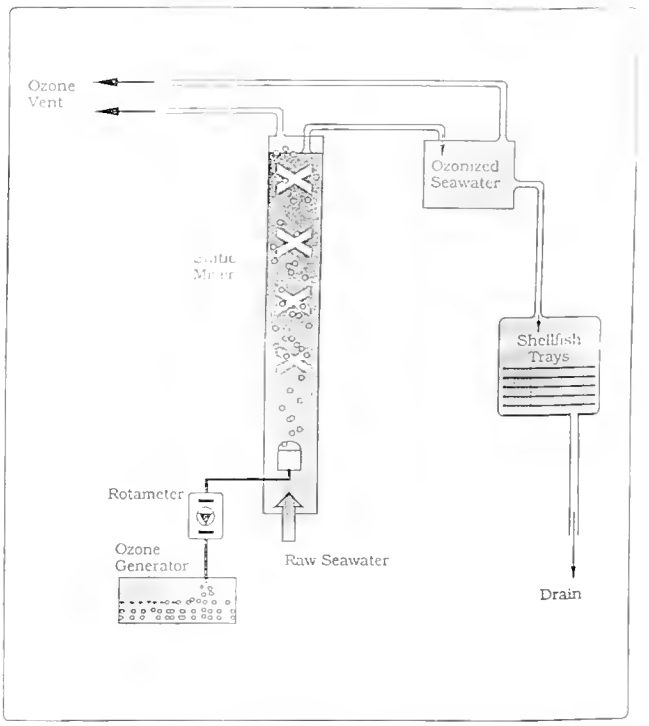

Figure 1. Ozone treatment apparatus for seawater contaminated by *Gonyaulax tamarensis (excavata)*. Ozone enters the Static Mixer and is mixed with seawater contaminated by *Gonyaulax tamarensis (excavata)* flowing up the mixer column. Ozonized seawater leaves the top of the column, is collected in a head tank, and gravity-fed to a series of fiberglass trays containing shellfish.

TABLE 1.

Ozone inactivation of dinoflagellate toxins as determined by mouse bioassay.

ml O_3/min	No. Mice	Death Time (min.)	% Survival (48 hr.)
	Gonyaulax tamarensis (excavata)		
220	5	—	100
110	10	—	100
55	10	12	90
27	10	12–14	20
0	20	5–6	0
	Gonyaulax catenella		
110	15	—	100
55	15	—	100
27	10	5–7	0
0	20	5–7	0

As indicated in Table 2, the New Brunswick *Mya arenaria* had an average PSP concentration of 260 μg/100 g meat (as judged by bioassay on mice) prior to experimental use. However, exposure to both the high and low ozone-dosed seawater produced a decrease in PSP levels within 24 hr. Both ozone doses detoxified these clams within 48 hr. to an acceptable level for human consumption. In contrast, control clams from this group, while showing a slow loss of PSP, did not approach toxin levels considered safe for vertebrates to consume, even after the 72-hr. PSP test period.

Previous unpublished studies with surf clams (*Spisula solidissima*), which had been exposed to high ozone doses of ~7.5 ppm for 2 weeks, revealed that experimental conditions induced metabolic stress. The *M. arenaria* samples examined during the oxygen consumption studies reported here, however, exhibited no respiratory alterations after ex-

TABLE 2.

Paralytic shellfish poison concentrations in *Mya arenaria* as judged by bioassay in mice.

	PSP concentration (μg toxin/100 g meat*)						
M. arenaria treated	T_0[a]	T_{24}	Detox. (%)	T_{48}	Detox. (%)	T_{72}	Detox. (%)
New Brunswick							
Oxygen control	260	234	10.0	108	58.5	125	51.9
0.5 ppm ozone	260	93	64.2	62	76.2	72	72.3
1.2 ppm ozone	260	78	70.0	69	73.5	74	71.5

* >80 μg toxin/100 g shellfish meat is the toxin level established as unsafe for human consumption by the U.S. Food and Drug Administration.
[a] T_x, where x = number of hours clam treated.
There is a ±10% precision inherent in the mouse assay, as performed by John Hurst, Jr., using Jackson Laboratory (Bar Harbor, ME) mice.

posure to low ozone doses. Respiratory values obtained were similar to reported values for this species at the same temperature and salinity under natural conditions (Thurberg et al. 1974).

In summary, laboratory and field investigations indicated that under the experimental parameters of toxin concentrations and ozonized seawater levels used, PSP inactivation could be achieved in bivalves exposed to and contaminated by motile dinoflagellate cells bearing PSP without measurably altering the physical state of the treated bivalves. Further, this inactivation could be achieved in a marketable species such as *Mya arenaria* within an economically feasible time structure (Blogoslawski et al. 1979). In related research, a preliminary report by Gacutan et al. (1984) suggested that ozone (and polyvinylpyrrolidone iodide–iodine) increased the detoxification rate of paralytic shellfish toxins in green mussels (*Perna viridis*), an important bivalve for human consumption in southeast Asia.

In the late 1970's (White et al. 1978, Anderson and Wall 1978) investigators began to examine more closely the dormant or encysted stage of the life cycle of dinoflagellates capable of producing PSP. While previously more attention was paid to the motile cells, due perhaps, to their creation of "colored" tides and dramatic toxic bivalve events, the ability of the organisms to pass into a cyst stage and become incorporated into the sediment became of increasing interest. Bivalves that pass most of their lives in nearshore sediments containing cysts with PSP could not escape ingesting toxic cysts and binding these small but steadily accumulated amounts of toxins into the tissues of the mollusks.

In 1982–84 work was begun on PSP inactivation tests with ozone gas for cyst-bound toxin. Soft-shell clams (*Mya arenaria*) at some locations in the southwestern Bay of Fundy have retained paralytic shellfish toxins continuously for the past several years, necessitating a year-round ban on harvesting. Promising results of earlier studies in Boothbay Harbor (Blogoslawski et al. 1979) prompted an investigation on the use of ozone to detoxify these shellfish. Clams were collected from Crow Harbour, New Brunswick, prior to each experiment and were separated by size and washed in the laboratory. Mean initial toxin content for each experiment was 264–274 μg STX equivalent/100 g. Clams were placed in trays of flowing seawater receiving dissolved ozone at four nominal concentrations (1.0, 0.7, 0.4, and 0.1 mg/l) or oxygen as a control. Duplicate samples were taken daily for '10-mouse' bioassay tests. Four experiments of 3–7 days' duration were conducted during the winter, spring, and autumn of 1983 at water temperatures of 4–7, 10–12, and 17–18°C, respectively. In none of the ozone treatments, nor in the controls, did detoxification occur.

Results indicate that ozonized seawater was ineffective in detoxifying *Mya arenaria* when the clams have come from areas where toxic cysts have been present in the sediments of the clam beds and the clams have retained toxins bound in their tissues for long periods (White et al. 1985).

PROS AND CONS

Cons

1. As reviewed above, ozonized seawater appears to be of no use in detoxifying cysts bearing PSP or in bivalves that have ingested cysts or have the toxin bound in their tissues over long periods of time. Whether detoxification can be achieved over a longer time frame or with different concentrations is of little value since it would not be economically feasible at this time.
2. Ozone gas is a powerful oxidant that can reach potentially harmful concentrations to humans though it is unlikely that this would occur in a detoxification or depuration set-up.
3. An ozonized seawater apparatus requires skilled technical maintenance and ambient water temperatures less than 40°C for proper contacting of the gas and water in order to achieve disinfection. (Blogoslawski and Monasterio, 1982).

4. The initial cost is high for the equipment.
5. The oxidant residual is difficult to measure or retain.

Pros

1. Ozonized seawater can detoxify PSP from motile dinoflagellate cells both in the laboratory as well as in situations where seawater is pumped ashore and treated or used for fish or shellfish culture.
2. Though not explored in this paper, ozonized seawater can be used as well to disinfect bacterial pathogens from hatchery-reared juvenile fish as well as depurate adult shellfish (Fauvel et al. 1979, ibid. 1982, Morrison et al. 1979, Abadie-Maumert et al. 1987).
3. The equipment is portable for small field studies or large stations can be established. Many prototype and state of the art ozone depuration stations exist for the treatment of contaminated shellfish.
4. The initial expense for the equipment is offset in the long term as no additional expensive chemical additions to the system are necessary (unlike chlorine stations).
5. Storage of large volume chlorine gas tanks is dangerous when leaks or accidents occur, unlike ozone gas which dissipates and breaks down to oxygen within 15 min. after the generator is shut off.
6. Ozonized seawater is useful in marine laboratories or aquaria that derive their seawater supplies from areas occasionally suffering from blooms of naked dinoflagellates. The use of ozonized seawater prevents the toxins from reaching vertebrate specimens. (Blogoslawski et al. 1975A).
7. Finally, ozonized seawater may be able to be used in areas not yet affected by cysts or bound toxins to open up a product for market that suffered from occasional or periodic toxic episodes caused by blooms of motile cells. In this way, a viable resource could be restored to the consumer.

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