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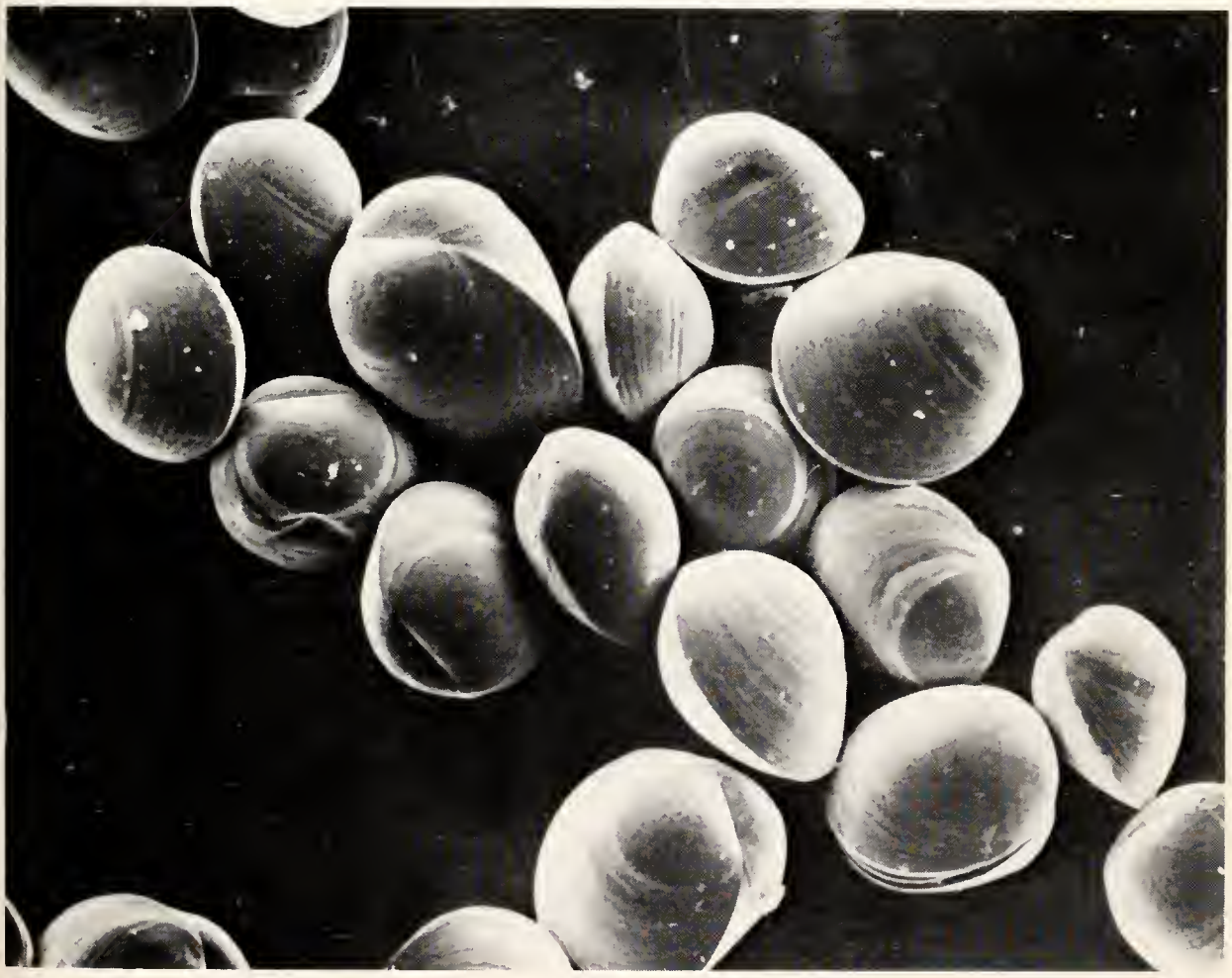

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Cover
Prodissoconch II stage larvae of the oyster, *Crassostrea virginica*
Courtesy M. R. Carriker and R. E. Palmer (See page 103).

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THE GRIT PRINCIPLE AND THE MORPHOLOGY OF OYSTER REEFS

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ABSTRACT

Old oyster reefs of the genus Crassostrea *form barren central ridges consisting of dead shell that may reach to the water surface and above. Some of the reef shell is as fine as flour and it varies upward in size to recently dead valves, but most of this material is of small size and is called grit. It is in constant motion on windy days and this scour prevents the settling of fouling organisms so that large areas of old shell remain bare except in deeper water on the flanks, where the effects of waves usually are not felt on the bottom. There live oysters grow.*

The grit principle explains the general structure of oyster reefs and their long existence as piles of dead shell until covered by sediment. Recognition of the grit principle explains many previously puzzling facts of live oyster and dead shell distribution. Examples are given. The grit principle was first deduced by the writer, but it was not observed or named. The working of the grit principle was first seen with SCUBA and named by C. L. Mackenzie. It can be observed in shallow water over any dead reef when the waves roll in.

INTRODUCTION

Oysters have been studied in considerable detail with regard to physiology, anatomy, developmental details, life history and related matters, all of which involve individual specimens primarily. Much less attention has been given to oyster reefs as ecological and even topographic entities. These are, nevertheless, matters of considerable importance.

Mobius (1877) first described the community aspect of organisms based on a reef of the European oyster, *Ostrea edulis* on the edge of the North Sea. He called the organization a biocenose. Caspers (1950) has shown that the original reef of Mobius has virtually disappeared. Presumably, it will leave a small and unimpressive geological relict.

In contrast, the large massive Gulf Coast reefs of *Crassostrea virginica* have been present during historical time and will doubtless last geologically for ages after being buried. I have pointed out before (Gunter, 1951) that *Ostrea* forms small encrusting reefs or banks, and *Crassostrea* forms large massive reefs consisting of large amounts of dead shell, and that this is a generic difference between the two groups.

Hedgpeth (1953, p. 164) says "The most characteristic and important biotic aggregation in the bays, both from the viewpoint of its effects on the physical environment as well as from that of human economics, is the oyster reef." His treatment of "The Oyster Biocenosis" is the most extensive since Mobius.

There are some strange inconsistencies and anomalies concerned with oyster reefs and dead oyster shell which for many years have puzzled

people who think about these matters. They have all fallen into place and the puzzles have been solved by what I am calling the grit principle of MacKenzie (1977) who first named it in print.

Oyster reefs and their origin and growth as reefs have been discussed by Grave (1905) and his theories and diagrams were repeated by Hedgpeth (1953, 1957), but these ideas have not been totally satisfactory to all students of the situation, possibly because Grave's reefs originated in shallow water. Be that as it may, the large massive oyster reefs that originate in subtidal water have been described in the words of Hedgpeth (*op. cit.*) as being "in cross section, a low mound with a high center or 'hogback' which is occupied by dead shells with live oysters on the sloping shoulders". This may be referred to as a mature or climax reef. There are many earlier intermediate stages, including perfectly flat beds of oysters covering large areas and without a ridge or even a shell bottom. Some oyster biologists do not consider such an agglomeration of oysters to be a reef and in the strictest sense that view is correct. It might be said that a climax oyster reef consists of a great deal of dead shell with a minor portion of living material. With these facts in mind it is easy to understand the workings of the grit principle.

BACKGROUND INFORMATION

I once published a little note (Gunter, 1938) which I later came to consider as one of my more important publications. It was never more than an abstract and it was not read. It came out in Proceedings of the Texas Academy of Science, a very out-of-the-way publication in those days; but I publicized it by energetic talking among my professional associates in oyster biology and shell dredging on the Gulf Coast. It stated in a few lines that buried oyster shell or mudshell, as the Gulf Coast shell dredgers called it, made good oyster cultch and oyster cultch was in scarce supply in those days, especially in south Texas where I sojourned.

As an aside I might point out that my late friend and colleague, Thurlow C. Nelson told me at the time that his father Julius Nelson had discovered the same thing with dead reef shell years ago in Barnegat Bay. I never found a printed reference to it in the New Jersey Experiment Station publications where Julius Nelson published most of his oyster work from 1889 to 1918 but it is no doubt true, for dead reef shell and mudshell are one and the same, one buried and the other not.

With my publication and announcement there began one of the puzzles. The state of Louisiana under the direction of Dr. Lyle St. Amant carried on experiments with the so-called new oyster cultch and found that it was highly successful. On the other hand, my former student and colleague Robert M. Ingle carried out experiments for the State of Florida with the mudshell cultch and had no success. This affair concerned one of the basics of oyster culture, spat collection, and it was a real puzzle.

Piles of shucked oyster shell on land, even if weathered for many years, will begin to smell and draw flies when the pile is dug into or uncovered so that the internal or covered parts come to the surface. It is also a well-known fact that shucked oyster shell when planted for cultch becomes covered with a bacterial slime and other organisms in a short while. Thus it may be said that shucked oyster shell is not good cultch because it permits fouling by bacteria and other slime-producing micro-organisms. Therefore, some years ago one of the chief problems of oyster culture was considered to be that of predicting spatfall with great accuracy so that clean unfouled shell would be planted and ready (Prytherch, 1928). Intensive studies of oyster spawning times and intervals to setting were made but there were few studies of fouling itself on oyster shells (Gunter, Dawson, and Demoran, 1957). Thus, the dry old reef shell has certain advantages because most of the organic material from the shell has been leached out or destroyed by bacterial action. Mudshell is also better cultch because it is smaller and also more fragile and breaks apart as the oysters grow and press against each other. For these reasons smaller clumps of oysters grow on it.

Then there are other puzzles. Why is it that old, dead reefs will build up with live oysters to be found only along the flanks and in deep water but with a central hogback or ridge growing in the midst of an essentially flat reef and even reaching the surface and above? These ridges are utterly barren. An example of such a reef is the Point au Fer reef in Atchafalaya Bay, Louisiana. Originally

it was approximately 30 miles long and was an agglomeration of dead shell rivaling in size the large coral reefs of the open oceans. This reef is now mostly covered with sediment from the Atchafalaya River. Not many other large reefs are left above ground in the natural condition. One is Hannah's Reef in Galveston Bay which is largely a pile of dead and barren shell. According to Eckhardt (1968) such material supports a lush jungle of growing organisms but nothing is further from the truth. Nothing grows there and nothing can grow there, which is part of the puzzle.

Then again I have seen the screen pile from shell dredges that worked on old reefs, Dog Island, Mad Island and Tiger Island, near the mouth of the Colorado River in Texas after it broke through the barrier islands. Here the old part of the reef near the surface was barren but the screen pile was studded with bits of oyster shell in mud, somewhat comparable to raisins in an English pudding, with small oysters growing on each piece of shell. Here was a reef of dead shell, on which nothing grew, within a few feet of oysters growing on pieces of old, dead shell which were dug from well within the same barren reef.

Similarly, in Mississippi waters screen piles near long dead reefs in the vicinity of Pass Marianne have caught oysters when no oysters grew on the exposed reefs. In this instance the people who opposed mudshell dredging railed against the dredges for sedimenting and killing the oyster beds which the dredging had created. This raised puzzles in my mind as to what processes went on which allowed a piece of shell dug from the middle of a dead reef to act as successful cultch while old, dead reef surface shell gathered no oyster spat. However, the idea was a misconception.

In the upper end of Galveston Bay, close to where Smith Point separates lower Galveston, I once observed another situation just as puzzling as the above. In former days there was a big, wide dead reef which ran all the way across the bay to Eagle Point on the western shore. Cattle crossed the bay on this reef seven miles to the western shore during low water periods. There were no oysters growing on it. The sharp shells of growing oysters would have precluded walking by cattle or horses or other large animals. The large reef had a small ridge of weathered, broken shell with a shallow area on each side. This little ridge came to the surface and on the south side of it there were no oysters, while on the north side where fresh water could bank up there were small but fairly scattered oysters. When the water was clear and still I could observe this situation very well. And so I came to the conclusion that there was not enough fresh water to permit oyster growth on the south side of the reef. But that conclusion was all wrong.

WORKINGS OF THE GRIT PRINCIPLE

Oyster shells do move and travel across the bottom carried by the currents and especially by wind-generated waves. This even happens to live and growing oysters when the winds are strong enough. For instance, in Copano Bay I have seen large, live, single oysters with pieces of attached algae washed up onto the beach, where they would eventually die. I have also mentioned before that on that windy coast you can find small oyster reefs by watching for spots of white shell on shore and running out from these points while poling the bottom in the direction of the prevailing winds, which in Aransas and Copano Bay is SSE. The simple reason is that the dead bits of shell are carried by the wind-generated waves from the reefs to the shore where they become stranded. Thus, the shell from an offshore growing reef collects on the strand in a rather restricted area. At the same time it will collect over a bottom roughened by the growth of oysters and eventually these shells will wash high enough to form a barren, central ridge of dead shell, but the barrenness is not caused by the currents or the waves except indirectly. Oyster shell crumbles and diminishes in size as it is dissolved, with the help of boring sponges, tunneling worms, boring clams, and such organisms, which may be present when the reef dies. There are also chemical reasons why the shell dissolves. The well-known result is crumbly shell, in small pieces ranging down to material known as flour and looking like flour in clear water when the wavelets wash in. However, most of this shell material is of a size called grit, and it moves up and down in a grinding, eternally restless motion caused by the unceasing waves of the sea. At times there are calms, but not long enough to make any dif-

ference, and we might say that as an oyster reef grows upward, its growth is limited by the grinding action of its own relict shell, which prevents the settling and fouling of any invertebrate larvae seeking a resting place, including larval oysters.

Mr. Clyde L. MacKenzie who has done a great deal of SCUBA diving in his examination of oyster reefs first observed this fact, so far as I know, and called attention to it in MacKenzie (1977). He pointed out that oyster spat would collect on large shells and oysters but not on grit at the same level or depth because the spat would be killed during windy periods, when the grit was in constant motion. I have since observed shallow dead reefs when the waves were barely breaking. Even so a cloud of "flour" wafts up and the small grit can be seen in motion. Observations can be made more easily with SCUBA gear close to the bottom on dead shell reefs.

This conclusion can be checked easily experimentally. However, the situation is much simpler than Langmuir's gyre, which was explained by observation alone, and in this case such experimentation would seem to be gilding the lily.

The conclusion also can be reached by simple deduction and in fact this has been done. After giving this paper at the New Orleans meeting of the National Shellfisheries Association (June 20, 1978), I returned home and revised it for publication. At that time I was surprised to find the following statement in Gunter (1972, p. 112), "Oyster reefs are composed of thick deposits of dead shell, some of them a few to several meters deep. They generally have a ridge or hogback with live oysters growing along the flanks. The hogback or central portion of a large old reef is made up of finely divided shell which moves with the wind and the waves and is even thrown up in ridges which project to the surface or even above it at moderate tides. This material is quite free of mud and it needs no washing when it is gathered. It is also free of sessile organisms. Quite probably this barrenness is due to the fact that this shell moves and is ground about by the wind and waves and any delicate larvae which would set in such a situation would soon be destroyed."

THE ANSWERS TO OLD PUZZLES

The barren areas on natural oyster reefs are caused by almost continuous grinding of the grit of broken down oyster shells caused by wave and wind action. This varies in depth, with exposure to wind sweep, protection of land, the presence of adjacent deep water or shallow water, prevailing wind direction and in fact all factors that influence the action of waves on the bottom. Obviously the depth and characteristics of the bare areas will be different at different depths on different reefs. In fact the topography of natural reefs can be related to the hydraulics of the bare areas and it is probable that the general setting of the whole reef can be related to a careful analysis of the live and dead areas of the reef.

The unsuccessful mudshell plantings by the State of Florida, mentioned above, were doubtless made in shallow water and probably also on hard bottom, where the particles of shell did not become immobilized and continued to bounce and grind with the waves, thus killing the larvae that set. This leads to the deduction that in planting mudshell for cultch the oysterman would do well to plant thinly on sticky bottom and not in solid layers of shell on shallow bottoms. In fact, successful plantings following these guidelines with mudshell have been made in Florida.

Dead reef shell from the center of an old reef holds oyster spat, while the surface of the same reef shows no set, as shown by the setting of oysters on screen piles on Dog Island Reef in Texas and near Pass Marianne in Mississippi. This might lead to the idea that some chemical effect is being exerted, but that is erroneous. The effect is purely mechanical. The purpose of screening on a shell dredge is to wash mud off the shell with a strong stream of water and then shunt the shell aside. Since the stream of water and sediment is now placed in the dredge cut, there is no screen pile deposited alongside and what remains today is only an area of mud with pieces of shell stuck in it, flush with the bottom. This attracts spat which live, while on the reef alongside, the spat are ground to death by the movement of the shell.

The observations made at Smith Point on Galveston, where no oysters were found on one side of a reef, may be explained by a long sweep of the bay from the south, where the waves piled in over the low flat reef keeping the grit in almost continual motion, while the other side of the reef was in the lee of the prevailing winds during the

warm season and there was not enough motion of the grit to prevent setting. The fact that there were some deeper reefs much farther south in Galveston Bay reinforces the conclusion that fresh water did not cause the difference.

LITERATURE CITED

Caspers, H. 1950. Die Lebenmeinschaft der Helgolander Austernbank. Helgolander Wissenschaftliche Meeresuntersuchungen.3:119-169.

Eckardt, B. 1968. Death of Galveston Bay. Transactions Thirty-third North American Wildlife and Natural Resources Conference. pp. 79-90.

Gunter, G. 1938. A new oyster cultch for the Texas coast. Proc. Texas Acad. of Sci. 21:14.

Gunter, G. 1951. The species of oysters of the Gulf, Caribbean and West Indian region. Bull. Mar. Sci. Gulf and Caribbean.1(1):40-45.

Gunter, G. 1972. Use of dead reef shell and its relation to estuarine conservation. Transactions of the Thirty-seventh North American Wildlife and Natural Resources Conference. pp. 110-121.

Gunter, G., C. E. Dawson and W. J. Demoran. 1957. Determination of how long oysters have been dead by studies of their shells. Proc. Nat. Shellfish. Assoc. 47:31-33.

Grave, Caswell. 1905. Investigations for the promotion of the oyster industry of North Carolina. Report of the U.S. Fish Commission for 1903. pp. 247-329.

Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. 3(1):107-224.

Hedgpeth, J. W. 1957. Chapter 23, Estuaries and Lagoons. II. Biological Aspects. pp. 692-729. Treatise on Marine Ecology and Paleoecology. Volume 1, Ecology. The Geological Society of America Memoir 67.

MacKenzie, C. L., Jr. 1977. Development of an aquacultural program for rehabilitation of damaged oyster reefs in Mississippi. Mar. Fish. Rev. 39(8):1-13.

Möbius, K. 1877. Die Auster und die Austernwirthschaft. Wiegandt, Hempel and Parry. Berlin. 126 pp.

Prytherch, H.F. 1928. Investigation of the physical conditions controlling spawning of oysters and the occurrence, distribution and setting of oyster larvae in Milford Harbor, Connecticut. Bull. U.S. Fish. Comm. 44:429-503.

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THE ABUNDANCE, DIVERSITY AND BIOMASS OF MACROBENTHOS ON NORTH INLET, SOUTH CAROLINA, INTERTIDAL OYSTER REEFS.[1]

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ABSTRACT

The seasonal abundance of macrobenthos varied from 2476-4077 m^{-2} with a maximum in early summer. Species number varied from 15-24 per sample with a total of thirty-seven species found. Nineteen species in North Inlet were common to Georgia and North Carolina oyster reefs.

INTRODUCTION

Oyster reefs are dense aggregations of not only oysters, but other benthic invertebrates which use oyster shell surfaces and the mud and crevices between shells as habitat. The reef organisms remove suspended particulate material from the water column and deposit this material on the bottom where it is further utilized by infauna. In addition, the reef organisms serve as a food source for transient predators of both aquatic and terrestrial origin.

Along the south Atlantic coast, the fauna inhabiting oyster reefs in North Carolina have been extensively described by Wells (1961). In South Carolina, Hopkins (1956) described some of the fauna of oyster reefs, emphasizing the boring sponges. Bahr (1974) in Georgia has quantitatively sampled intertidal oyster reefs. The reefs described by Bahr are very dense rock-like mounds, known locally as oyster rocks and common to open water while reefs in South Carolina tend to be more muddy forming finger like extensions into tidal creeks and bordering the salt marsh-creek interface (Dame, 1976).

In South Carolina, approximately 95% of the natural oyster grounds are intertidal while only 5% are subtidal. At North Inlet, near Georgetown, South Carolina, the intertidal oyster populations, which cover approximately 5% of the area, reach very high densities, 1000-2000 m^{-2}, and energy flow approaches 10,000 kcal $m^{-2}yr^{-1}$ (Dame, 1976). The purpose of this study was to determine the abundance, diversity and seasonality of the organisms inhabiting these oyster reefs with the hope of better understanding the role these organisms play in the intertidal oyster reef and in the marsh- estuarine system. In addition, information is presented for intertidal reefs which clarifies Wells' (1961) hypothesis that oyster reef fauna are richer in higher salinity areas.

[1]Contribution No. 262, Belle W. Baruch Institute for Marine Biology and Coastal Research.

TABLE 1. *Seasonal abundance and species diversity of macrofauna on North Inlet intertidal oyster reefs.*

Species	No. m^{-2} 7/74	9/74	11/74	1/75	3/75	5/75	8/75
Polychaeta							
Amphitrite ornata	4	4	25	20	17	38	
Cirratulus grandis		43				13	12
Glycera americana	1	1	13			13	1
Heteromastus filiformis	337	312	818	956	826	1867	1098
Hydroides dianthus					4		
Laeonereis culveri					1		
Lumbrinereis tenuis				13			295
Marphysa sanguinea	7	7		26	1		3
Nereis succinea	142	107	96	234	240	72	58
Paleanotus heteroseta		1					
Panopea bitruncata						1	
Pectineria gouldii				25			
Pherusa sp.		1					
Phyllodocea fragilis	8	7	15	13	5	13	8
Polycirrus eximius						1	
Polydora ligni				25			
Scoloplos fragilis		1		13	13	38	
Streblosoma sp.					1		
Arthropoda							
Anurida maritima	27	7	7				
Balanus eburneus		34	30	40	66	30	54
Eurypanopeus depressus	114	46	22	12	29	29	94
Gammarus palustris	2		17	18	3		
Insect pupae	6	3	3	76	102	52	
Melita nitida	7	4	11	15	44	64	14
Panopeus herbstii	65	88	14	31	13	5	79
Pinnotheres ostreum			1				
Uca pugilator		11				38	
Mollusca							
Brachidontes exustus	778	712	732	403	654	780	872
Chione intapurpurea		1				1	
Crassostrea virginica	1139	1058	725	489	584	708	915
Geukensia demissa	6	8			10	1	21
Ilynassa obsoleta				13			
Mercenaria mercenaria	6	5					
Odostomia impressa			55	116	150	224	4
Terrebra dislocata			3				
Nematoda		1					
Nemertea		14		17	13	89	
Total Individuals	2649	2476	2587	2555	2776	4077	3525
Total Species	16	24	17	20	19	21	15
H′ (Diversity Index)	1.52	1.62	1.60	1.96	1.89	1.69	1.69

MATERIALS AND METHODS

Over 13 months (1974-1975), bimonthly samples were taken from several intertidal oyster reefs in North Inlet, South Carolina. The reefs used were divided into ¼m x ¼m quadrants, each quadrant was assigned a number, and at each sampling four quadrants were chosen for collection using a list of random numbers. All material within each quadrant was completely removed by shovel to a depth of 0.3m and sediment immediately sieved through a 1mm stainless steel screen. Soft bodied organisms were temporarily preserved in buffered formalin. The soft bodies of bivalve molluscs were removed from the shell and dried. After identification and enumeration, all organisms were dried to a constant weight in an oven at 60 °C.

RESULTS

A total of thirty-seven species of marcrobenthos were collected over the time period sampled. The number of species collected per sample period varied from 15-24 with no discernable seasonal trends (Table 1) and the number of individuals ranged from 2476-4077 m^{-2} with a maximum in early summer and a minimum in winter.

The Shannon diversity index (Shannon and Weaver, 1963) was computed from the data in Table 1 and varied from 1.52-1.96 with a maximum value in winter samples.

The dominant filter feeding bivalves, *Crassostrea virginica, Brachidontes exustus,* and *Geukensia demissa,* showed a seasonal trend in numbers m^{-2} with a maxima in summer and a minima in winter. The carnivorous decapod crustaceans, *Panopeus herbstii* and *Eurypanopeus depressus,* showed seasonal trends similar to the bivalves. The predominant polychaete worms, *Amphitrite ornata, Heteromastus filiformis, Nereis succinea, and Phyllodocea fragilis,* showed a reverse trend with maximal densities in the winter and minimum numbers in the summer. The amphipod, *Melita nitida,* seems to show trends in abundance similar to the polychaetes.

Several species were only found during certain seasons. Both the gastropod, *Odostomia impressa,* and the polychaete, *Scoloplos fragilis,* were found in the cooler months of the year. Another polychaete, *Glycera americana,* was only found in winter.

The biomass of dominant macrofauna is shown in Table 2. Seasonal biomass trends are only seen in the amphipod, *Melita nitida,* the gastropod, *Odostomia impressa,* and the polychaete, *Nereis*

TABLE 2. *Dry weight biomass* of the dominant macrofauna on intertidal oyster reefs.*

	g m^{-2}						
Species	7/74	9/74	11/74	1/75	3/75	5/75	8/75
Amphitrite ornata	0.400	0.596	2.730	0.159	0.109	0.483	
Brachedontes exustus	4.670	4.400	4.350	1.543	3.830	4.891	5.593
Crassostrea virginca	195.879	183.114	115.500	112.624	162.357	130.760	125.400
Eurypanopeus depressus	4.390	11.690	1.013	4.356	15.431	1.634	2.522
Gammarus palustris	0.002		0.028	0.597	0.076		
Geukensia demissa	0.640	1.060			0.284		3.747
Glycera americana	0.002	0.046	0.013			0.012	0.005
Heteromastus filiformis	0.030	0.409	1.850	0.262	0.168	1.956	0.004
Insect pupae	0.006	0.037		0.027	0.041	0.007	
Marphysa sanguinea	0.153	0.207		0.015	0.025		0.248
Melita nitida	0.007	0.069	0.013	0.305	0.175	0.037	0.028
Nemertean		0.014		0.167	0.003	0.088	
Nereis succinea	1.200	0.507	0.495	9.656	42.754	0.575	0.328
Odostomia impressa			0.102	8.196	11.360	2.239	0.038
Panopeus herbstii	6.370	10.998	0.308	6.855	17.386	1.688	1.070
Phyllodocea fragilis	0.068	0.116	0.048	0.001	0.762	0.039	0.047
Scoloplos fragilis		0.009		0.001	0.001	0.038	

*soft body for bivalves

succinea, all of which have higher values in the winter than in other seasons.

DISCUSSION

The fauna of the intertidal oyster reefs of North Inlet are both abundant and diverse, and there are differences between the fauna described here and that found in North Carolina and Georgia. In North Carolina, Wells (1961) reported a total of 303 species collected from both intertidal and subtidal oyster reefs progressing up the Newport River. Two sites in Wells' study are mainly intertidal oyster reefs — Shark Shoals and Sluiceway. These areas showed an average number of 55-65 species which is considerably more than the 18.9 species found per collection in the North Inlet study. Thus the data from the high salinity ocean dominated intertidal oyster reefs of North Inlet do not support Wells' contention that oyster reef fauna are richer in higher salinity waters. One possible explanation for this discrepancy may be that Wells in his study was sampling subtidal shell bottoms adjacent to intertidal oyster reefs. In North Inlet, such shelly bottoms are almost devoid of living oysters but have a rich fauna averaging 51.7 species per sample (Dame, unpublished).

In Georgia, Bahr (1974) found a total of 42 species of macrofauna on the intertidal oyster rocks of the Duplin River, a number very similar to the 37 species found in North Inlet. In addition, diversity as measured by the Shannon Index was almost the same in both areas; i.e., 1.5-2.2 for Georgia and 1.52-1.96 for South Carolina. However, one glaring difference does occur —the average density of macrofauna in Georgia was 24,747 individuals m^{-2} compared to 2949 individuals m^{-2} in North Inlet. This difference may be explained by sampling technique, since Bahr used a 0.5mm mesh screen for sieving, and by the difference in the oyster rock habitat to the muddy reef. In contrast, biomass estimates were similar in both areas when shell organic carbon is taken into account.

It is well known that sieve size influences the number of organisms collected, but in a recent review by Maurer (1977), he found more than half of the macrobenthic studies conducted recently in the Virginia to Massachusetts area used sieve sizes 1mm or larger. Caution should be taken when looking at the seasonal trends of smaller organisms such as polychaetes and amphipods, which can show high densities when sieved through screens less than 1mm.

A list of the macrofaunal species common to North Carolina, South Carolina and Georgia intertidal oyster reefs is presented in Table 3. These macrofauna are represented functionally by filter feeders, deposit feeders and predators which together form one of the highest energy flux heterotrophic systems known (Bahr, 1974; Dame, 1976). The intertidal oyster reef is structurally distinct and functionally can be very important in estuaries. It is crucial therefore that the abundance and species composition of specific oyster reef systems be determined in any comprehensive study because there are considerable differences in different environmental settings.

TABLE 3. *Macrofauna common to North Carolina, South Carolina and Georgia intertidal oyster reefs.*

FILTER FEEDERS
Balanus eburneus
Brachedontes exustus
Crassostrea virginica
Geukensia demissa
DEPOSIT FEEDERS
Amphitrite ornata
Anurida maritima
Gammarus paulustris
Glycera americana
Heteromastus filiformis
Marphysa sanguinea
Melita nitida
Neries succinea
Phyllodocea fragilis
Polydora ligni
PREDATORS
Eurypanopeus depressus
Nemertea
Odostomia impressa
Panopeus herbstii
Pinnotheres ostreum

ACKNOWLEDGMENTS

I would like to thank L. Lovell and W. Mertashaw for their help in collecting and identifying the oyster reef samples. Dr. D. Dauer checked the

identification of the polychaetes. I am also indebted to Dr. B. Coull for reading an early draft of this manuscript and offering many useful suggestions. The work reported here was supported by EPA contract No. R-802928.

LITERATURE CITED

Bahr, L. M. 1974. Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph. D. Dissertation, University of Georgia. 149pp.

Dame, R. F. 1976. Energy flow in an intertidal oyster population. Est. Coastal Mar. Sci. 4:243-253.

Hopkins, S. H. 1956. The boring sponges which attach South Carolina oysters, with notes on some associated organisms. Contributions from Bears Bluff Laboratories No. 23.

Maurer, D. 1977. Estuarine benthic invertebrates of Indian River and Rehoboth Bays, Delaware. Int. Revue ges. Hydrobiol. 62:591-629.

Shannon, C. E. and W. Weaver, 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana. 117pp.

Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31:239-266.

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THE USE OF SONIC GEAR TO CHART LOCATIONS OF NATURAL OYSTER BARS IN LOWER CHESAPEAKE BAY[1,2]

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ABSTRACT

An underwater microphone has been developed to detect shell material on the bottom. The system is simple to use and easily constructed. It consists of a microphone encased in a PVC tube and suspended from an A-frame which is towed over the bottom. It is being used along with other methods to chart oyster bottoms in Virginia.

INTRODUCTION

A comprehensive survey of the location and extent of Virginia's natural oyster bars in Lower Chesapeake Bay was started in 1976 by the Virginia Institute of Marine Science. Its objective was to delineate on charts the location of naturally or potentially productive areas within the bounds of Virginia's 243,000 acres of designated public bottom (Baylor, 1894). The 1894 Baylor Survey set aside large areas for public use in the estuaries and included much of the State's naturally productive bottoms. In addition, however, it contained extensive areas which were unsatisfactory for oyster culture (Moore, 1910; Haven, Hargis and Kendall, 1978). In view of this situation, it is essential for management purposes to chart the productive and unproductive areas within the survey area. The sonic gear described in this paper was designed to aid in charting the productive and unproductive areas.

The characteristics of productive oyster bottoms have been described by earlier investigators (DuMont, 1950; Galtsoff, 1964; Chestnut, 1974). Based on these attributes, the following classification was used in our study. In Lower Chesapeake Bay productive or potentially productive areas are defined as those presently having significant quantities of exposed or buried shell or living oysters. Areas lacking living oysters or shells in the substrate, generally sand or mud bottoms or those deeper than 9 m, are considered nonproductive or as having a low potential for oyster culture.

Previous surveys have delineated productive oyster bottoms using several techniques. Early studies in Maryland used a dredge to locate concentrations of shells and oysters (Frey, 1946). Later, Maryland researchers investigated the use of side-scan sonar (Balderson, *et al.*, 1974). The Maryland Department of Natural Resources recently began a bottom survey using patent tongs, fathometer, and a probe to determine

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[1] *Contribution No. 890 from the Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.*

[2] *Research sponsored by NOAA, National Marine Fisheries Service, Contract No. 3-265-R-1.*

oyster density. The underwater microphone described here is used as an aid in locating oyster beds (Harold Davis, personal communications). A study in South Carolina located oyster beds by dragging a chain astern of the vessel and detected shell by the vibrations in the tow rope (Keith and Cochran, 1968).

The present paper deals with the design of a unique underwater microphone which will detect oyster and shell deposits acoustically. When towed over the bottom, the device enables an operator to detect areas of exposed shell as distinct from sandy bottom or soft mud on the basis of sound characteristics. It presently is being used in conjunction with an electronic positioning gear and other methods to delineate natural oyster bottoms.

METHODS

The positioning system used to locate sampling areas is manufactured by the Teledyne Hastings-Raydist Corporation, Hampton, Virginia. It utilizes four transmitting stations and a receiver (navigator) located in the research vessel. The navigator shows the boat's position within ± 2 m as a series of numbers on a grid system which are related to latitude and longitude.

As the research vessel is steered along a grid transect with the aid of the navigator, the vessel operator listens to the sonic gear speaker and records the percentage of time he hears the microphone impacting on shells or oysters. At the same time an experienced waterman probes the bottom at intervals of about 75 m with a long aluminum pole and reports the bottom type as shell, mud and shell, sand and shell, sand, mud, buried shell, clay, etc. This information, along with the data on depth obtained with a fathometer, is coded and entered into a printer which also records the boat's position in terms of grid coordinates. A survey using a bottom grab verifies bottom type as shown by the sonic gear and the probe. Later, all information is plotted on a chart which shows transects, station locations, bottom type, percent shell, and depth.

The sonic gear towed over the bottom consists of an A-frame about 3 m high and 2 m across the base. Suspended from each leg of the frame are 2 m of heavy chain. The microphone is attached to the center of the crossbar by 15 cm of flexible stainless steel cable. The microphone is encased in 2.5 cm diameter PVC pipe 25 cm long. One end is capped; the other end has a cap drilled to take one end of a 60 m length of coaxial cable (RG-58). The pipe enclosing the microphone unit is water- proofed and surrounded by a 1 kg cylindrical zinc weight (Figure 1). The coaxial cable leading to the vessel is loosely attached at intervals to a stainless steel towing wire. For uniform performance of the microphone unit, it is suggested that the cylindrical zinc weight, the length of stainless steel cable from the crossbar to the microphone, and the length and weight of the chain not be changed during any survey.

The schematic for the amplifier and speaker located in the cabin of the vessel and their aux-

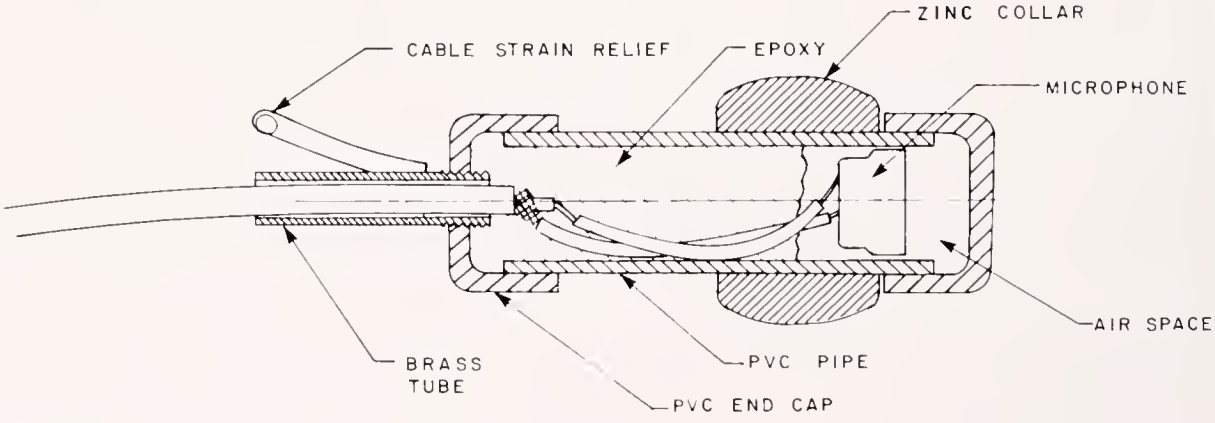

FIGURE 1. *Details of the microphone unit enclosed in PVC pipe.*

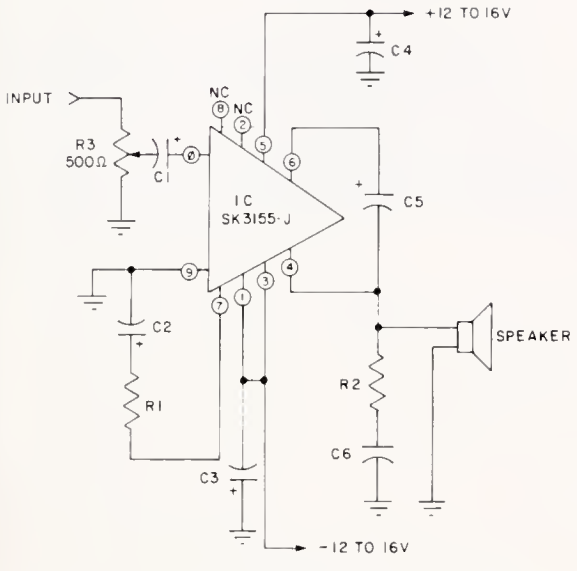

FIGURE 2. *Details of the amplifier system and speaker.*

iliary components are shown in Figure 2. The speaker unit has an output of 13 watts and 12 volts; the system is powered by two 12-volt dry batteries.

The A-frame with the attached microphone is towed at a speed of 3 knots. At this speed, the two chains are of sufficient length and weight to keep the microphone on the bottom. Dragging the sensor over the bottom causes the amplifier to emit characteristic sounds for the different types of materials it impacts.

RESULTS AND DISCUSSION

When the microphone unit is dragged over the bottom shell, oysters, or similar material, it causes an irregular series of sharp bumping sounds on the audio which range from a continuous roar for dense shell bed to an occasional click when the unit hits an isolated shell. Over a sandy bottom a hissing sound is heard. Stones or other material give a slightly different sound. No sound is heard when the bottom is soft mud. With experience, the operator becomes able to detect many subtle differences.

The superiority of the underwater microphone in detecting shell material over the conventional probe is shown in Table 1. Probing the bottom

TABLE 1 *Comparison between detection of shell by a probing aluminum pole and the underwater microphone on an oyster rock in the Rappahannock River, Virginia.*

Estimated percent of time shells heard on audio between stations	Number of stations probed	Number of times probe failed to find shell	Percent agreement
1-20	39	18	46
20-50	47	2	96
50-75	36	1	97
75-100	12	0	100

may fail to show shell where shell is widely scattered. That is, the underwater microphone shows what type of distribution exists between the probed locations.

The unit described is simple to construct and easy to use; it is relatively inexpensive. Alternate methods of detecting the presence or absence of shell such as dragging a chain requires more effort. Side-scan sonar, while effective in some areas, is expensive and cannot distinguish between sand and mud bottoms. Moreover, it gives a less precise location of the beds than may be obtained with the towed sonic gear.

LITERATURE CITED

Balderson, R. H., N. H. Kenyon, A. R. Stride and A.H. Stubbs. 1972. Sonographs of the sea floor. National Institute of Oceanography. Wormley Godalming, Great Britain. The Elsevier Publishing Co.

Baylor, J. B. 1894. Method of defining and locating natural oyster beds, rocks and shoals. *In* Oyster Records (pamphlets, one for each Tidewater, Va. county, which listed precisely the boundaries of the Baylor Survey). Board of Fisheries of Virginia.

Chestnut. A. F. 1974. Oyster Reefs. In: Coastal Ecological Systems of the U.S. Ed. H.T. Odum, B. J. Copeland and E. A. McMahan. Pub. Conserv. Found., Washington, D.C. P. 171-203.

DuMont, W. D. 1950. Report on various tests on bottoms for oyster planting. Proc. Natl. Shellfish. Assoc. P. 42-48.

Frey, D. C. 1946. Oyster bars of the Potomac River. U.S. Dept. of the Interior, Special Sci. Rept. 32. 92 p.

Galtsoff, P. S. 1964. The American Oyster *Crassostrea virginica* Gmelin. U.S. Fish. Wildl. Serv. Fish. Bull. 64:1-480.

Haven, D. S., W. J. Hargis, Jr., and P. C. Kendall. 1978. The oyster industry of Virginia: Its status, problems and promise. VIMS Special Papers in Marine Science No. 4. Va. Inst. of Mar. Sci., Gloucester Point, Va. P. 1-1024.

Keith, W. J. and H. S. Cochran, Jr. 1968. Charting of subtidal oyster beds and experimental planting of seed oysters in South Carolina. Cont. Bears Bluff Lab. No. 48. P. 1-19.

Moore, H. F. 1910. Condition and extent of the oyster beds of James River. U.S. Bur. Fish. Doc. No. 729, Washington, D.C. 83 p. plus charts.

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GROWTH, RECOVERY, AND MOVEMENT OF MANILA CLAMS, *VENERUPIS JAPONICA* (DESHAYES) AT SQUAXIN ISLAND, WASHINGTON[1], [2], [3]

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ABSTRACT

Manila clams, Venerupis japonica, *averaging 3 mm were planted in May, 1976 and May, 1977 at a density of 284/m² and were monitored for growth and recovery for up to 16 months. Successful marking was accomplished by spraying flourescent paint on at least one valve of each clam. Protective mechanisms to improve recoveries were tested, and both plastic netting and wire cages increased recoveries significantly. A series of migration studies was conducted and showed that seed clams move across the beach and can be stopped and concentrated by small mesh fences or plastic netting laid flat on the beach. Naturally set clams can be concentrated in a similar manner. The netting also tended to improve growth rates, thus providing additional benefit.*

INTRODUCTION

For several years the College of Fisheries at the University of Washington has been studying the potential for increasing natural populations of Manila clams (*Venerupis japonica*). Holland and Chew (1973) studied the reproductive cycle of *V. japonica* in Puget Sound. Jones (1974) examined early mortality and growth of hatchery-reared seed clams planted in Washington waters. Since that time most research has involved spreading small (3-15mm) clams on beaches having various natural densities of clams. Chew (1975) reported the progress and prospects of this approach to improving clam populations, and Miller of the University of Washington (personal communication) has continued this research at five study sites in Puget Sound. One of the striking characteristics of clam seeding experiments has been low recovery rates. Several hypotheses for this have been advanced. Gaumer (1976) suggested that beach slope and wave exposure are important factors, but he noted that movement of clams may also be important. Both Gaumer (1976) and Magoon of the Washington State Department of Natural Resources (personal communication) have observed the tracks of the Manila clams across the surface. Miller et al. (1978) stated that tidal height, substrate composition and predation are other important factors. This field study at Squaxin Island was designed to differentiate the causes of the low recovery rates.

MATERIALS AND METHODS

Site Description

Experimental plots were constructed at three sites on Squaxin Island in south Puget Sound

[1] Contribution No. 502, College of Fisheries, University of Washington
[2] This study was supported by a grant from the Squaxin Island Indian Tribe
[3] The work reported here was part of a thesis submitted by the senior author to the Graduate School, University of Washington, in partial fulfillment of the requirements for the Master of Science Degree

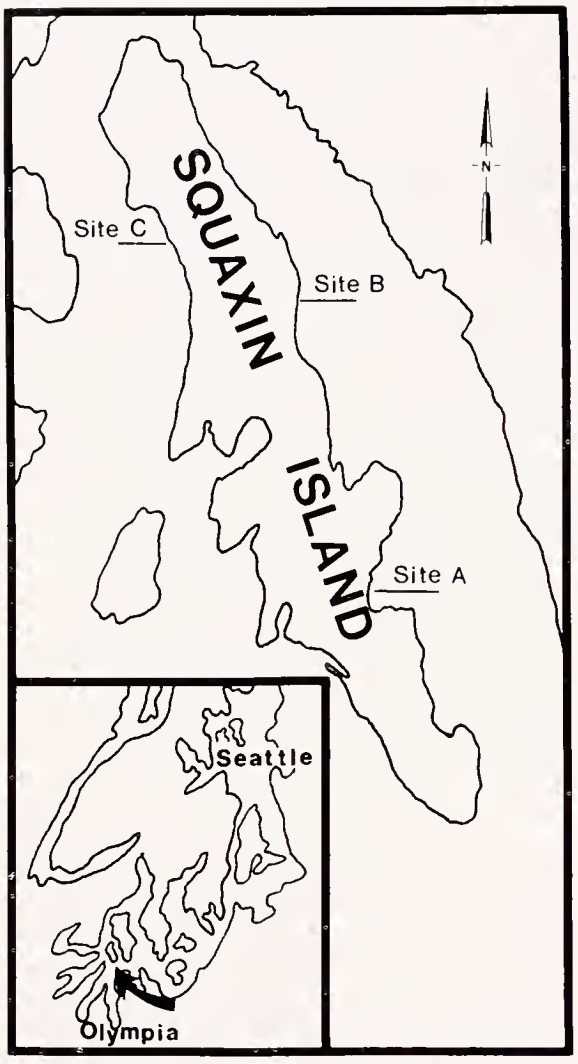

FIGURE 1. *Map of Squaxin Island showing location of experimental clam reseeding sites.*

(Figure 1). The sites differed in natural densities of clams, substrate type, and beach slope. Site A had many naturally occurring Manila clams and a shell/gravel substrate. Site C had no Manila clams, few clams of any other species and the substrate was mostly loose gravel and coarse sand. Site C had more intensive wave action and exposure than the other two sites.

A 20m x 10m study plot was established at each site (Figure2), and a 3m x 3m plot was constructed about 5m seaward to extend the tidal range covered by the study. The two plots at Site A extended from 2.5 to 7.5 feet above MLLW, at Site B from 1.5 to 8.0 feet, and from 2.0 to 8.5 feet at Site

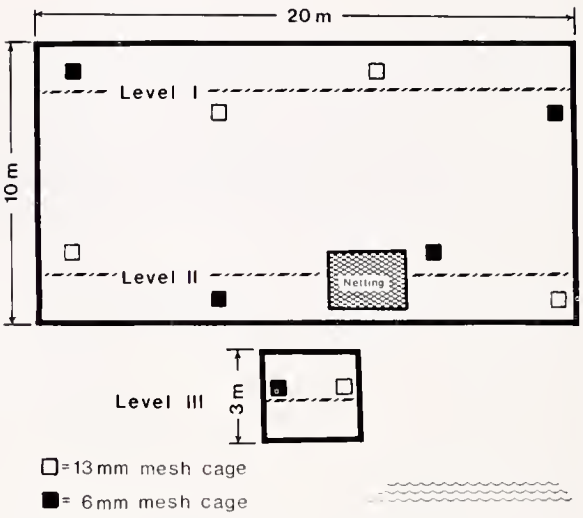

FIGURE 2. *Design of the experimental plot at each of the three study sites.*

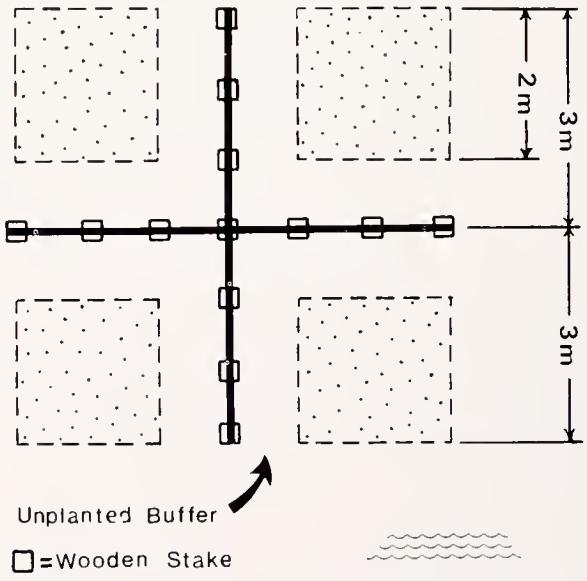

FIGURE 3. *Design of 3mm mesh plastic netting fence study at Sites A and C. Stippled areas indicate areas planted at 284 clams/m² in May, 1977.*

C. Large plots were not used at the lower level because of the abundance of moon snails (*Polinices lewesi*), a clam predator. Eight 0.8m x 0.5m wire mesh cages of 13mm or 6mm mesh were placed on the large plots and two cages were placed on the smaller plots to exclude predators. A 2m x 3m section of 6mm mesh plastic netting was

secured to an area of each large study plot. Site C had two additional 3m x 3m plots which were covered with a layer of large cobble and coarse gravel in an effort to stabilize the substrate.

A 30cm high fence of 3mm mesh plastic netting was constructed in the shape of a cross near the plots at Site A (Figure 3). The 3m arms of the fence were designed to detect movement of clams both horizontally and vertically across the beach. The bottom edge of the netting was buried 3 to 5 cm to prevent movement of clams below the surface. Each quadrant was seeded in May, 1977 with marked clams, leaving a 1m wide unplanted buffer along each side of the fence. Samples were taken from both planted and buffer zones.

Description of Seed Clams

Manila clam seed was obtained from Pacific Mariculture, Inc., at Moss Landing, California. Average seed size was 3mm. In 1976, the clams were stained with a red calcium dye (Alizerin Red-S), but this marking method was not successful. In 1977, seed clams were sprayed with fluorescent orange paint. This method was effective in marking clams for the duration of the study and the positive identification was simplified by use of a UV "black light". The marked clams were planted in May, 1977 at a density of 284 per m^2 (an average density for commercially dug areas) by sprinkling them by hand just as the tide covered the plots.

Sampling

Three transects were established across the plots parallel to the water at estimated tidal heights of 7 to 8 feet above MLLW for Level I, 5 feet for Level II, and 2 to 3 feet for Level III. Samples were taken from either side of these lines, from the cages, and from the plastic netting. All Manila clams collected during the 15 month study were measured to 0.1mm and a series of length-frequency diagrams were constructed to aid in determining growth. This was especially helpful at Site A where wild clams were frequently encountered.

One-way analysis of variance was performed on the data from the 1976 planting to compare the size of clams after 15 months of growth at the three sites. A 2 x 2 factorial design was used to compare size of clams by beach and treatment (tidal height or netting), and a similar design was used to compare recovery densities.

RESULTS

Growth of Clams

Growth rates differed significantly between beaches and treatments. Only the data from the 1976 planting is discussed due to the short duration of the 1977 study. Length-frequency distributions of clams under netting at Site C are shown in Figure 4. Since no wild clams were present at Site C, this figure reflects only planted clams. Maximum growth of clams at all locations occurred during the late summer and fall, and little or no growth occurred during winter. Figure 5 shows the average length of clams at each sampling time. After 15 months there was no significant dif-

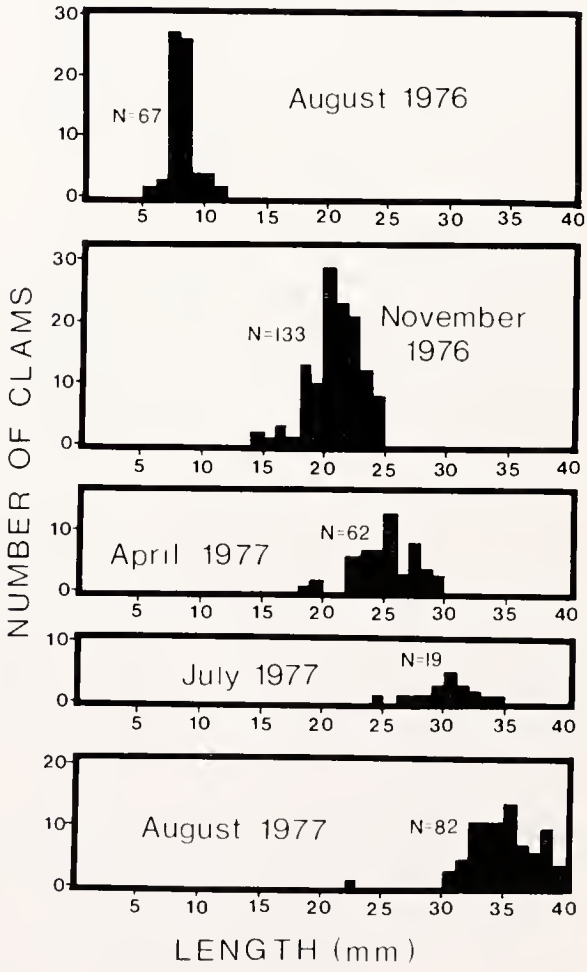

FIGURE 4. *Length-frequency distribution of clams found under plastic netting at Plot C at each sample time.*

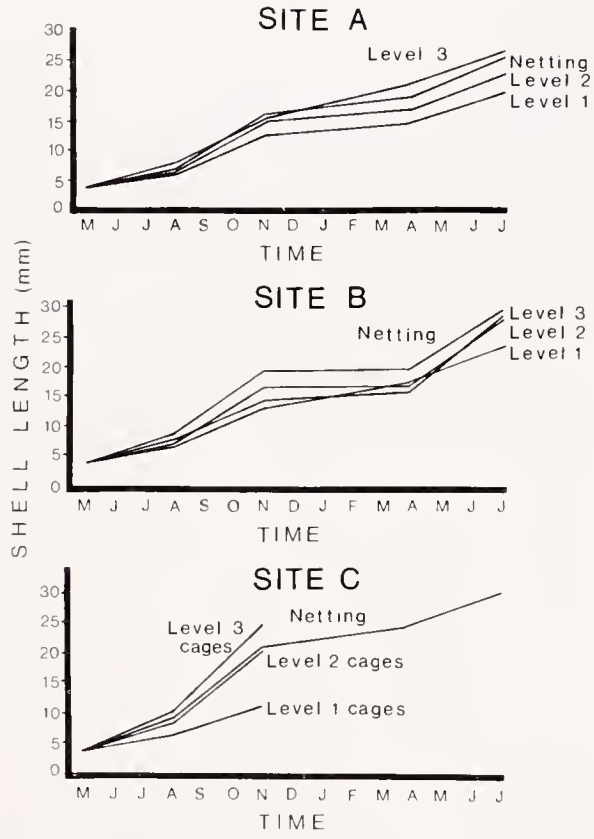

FIGURE 5. *Average size of clams at each sampling time. (Sites A and B show unprotected and netting areas. Site C shows netting and cages due to absence of clams in unprotected areas.*

ference in size of clams under netting at Sites B and C, which averaged 29.3 and 30.3mm respectively (Table 1). Clams under netting at Site A averaged 25.7mm, significantly less than the other sites (alpha = .05). More rapid growth was noted at lower tide levels, especially at Sites B and C. Coverage of the beach with plastic netting enhanced growth.

Recovery of Clams

Since movement of the clams was extensive, the term "recovery" will be used rather than "survival". No studies to date have determined actual survival rates, and the study was not designed to distinguish between survival and migration.

Overall clam recoveries were higher between the 5 to 8 foot tidal levels. There was no significant decrease in recoveries over time (alpha = .36), but treatment effects were significant (alpha = .05). The best recoveries were consistently found under the cages or netting (Table 2). After 15 months, recoveries ranged from 2.8 to 60.6 percent in unprotected areas, and 38.8 to 73.8 percent under cages or netting at Sites A and B. At Site C recoveries were 0 percent and 96.8 percent in unprotected and protected areas respectively. The high recoveries under the netting at Site C may have been due to immigration of clams planted nearby.

The substrate modification plots at Site C were

TABLE 1. *Average length of clams in mm 15 months after planting.*

	SITE A			SITE B			Site C		
Tide Level	Cages	Net	Unprotected	Cages	Net	Unprotected	Cages	Net	Unprotected
Level I	19.7	NT	20.0	25.4	NT	23.8	ID	NT	ID
Level II	25.2	25.7	23.1	32.8	29.3	28.3	ID	30.3	ID
Level III	31.3	NT	26.5	28.1	NT	28.6	ID	NT	ID

NT =not tested in this study
ID=insufficient data for analysis

TABLE 2. *Range of recoveries in percent 15 months after planting.*

	SITE A			SITE B			SITE C		
Tide Level	Cages	Net	Unprotected	Cages	Net	Unprotected	Cages	Net	Unprotected
Level I	71.4	NT	24.2-51.4	55.3	NT	20.4	ID	NT	0
Level II	46.7	73.8	37.6-60.6	44.9	47.2	5.6	ID	96.8	0
Level III	38.0	NT	8.4	38.0	NT	2.8	ID	NT	0

NT=not tested in this study
ID=insufficient data for analysis

abandoned after four months due to low recovery rates. Control areas had 0 percent recovery, and although cobble improved recoveries, the 10 percent recovery rate was not sufficient to warrant further testing.

Movement of Clams

Considerable shoreward movement of small clams occurred at Site A within six weeks after the 1977 planting. The cross-shaped fence tended to block this movement. On the bay side of the fence, the density inside the planted areas was 98/m^2 while the unplanted buffer had up to 138/m^2. Above the fence the density in the planted areas was 206/m^2 with up to 59/m^2 in the buffer. Small wild clams were most abundant in the buffer below the fence also, with densities of up to 118/m^2.

A similar concentration of small clams was observed in 1977 under and near the plastic netting which had been layed on the beach the previous year. Densities of small wild clams beneath and just seaward of the netting ranged from 350 to 600/m^2, whereas other areas on the beach showed a setting density of 20 to 80/m^2.

DISCUSSION

Most of the variation in growth among the study sites can be attributed to tidal height. Within each study plot, growth was more rapid at lower tide levels due to longer submergence periods. An unexpected result was that coverage by plastic netting and cages also increased clam growth over other areas at the same tide height. A possible explanation is that increased substrate stability allowed the clams to expend energy on growth rather than on maintaining their position in the substrate. Although growth was faster at lower tide levels, recoveries were better at higher tide levels, especially from about 5 to 8 feet above MLLW. This is the tidal height that Quayle and Bourne (1972) considered optimum for Manila clams in British Columbia. Both cages and netting improved recoveries over unprotected areas, often dramatically. At Site C the netting maintained recoveries of over 90 percent for 15 months, while no clams were found in unprotected areas. The loose gravel substrate at this site was unsuitable for clam seeding unless protective devices were added. This observation supports the hypothesis that substrate stability is important for clam production, and that plastic netting provides this stability.

Recoveries under netting of over 100 percent were observed, which indicates immigration of small clams also occurs. Once the clams are too large to pass through the 6mm mesh, however, no movement can occur, and this probably accounts for much of the improvement in recovery over unprotected areas. Netting also tended to concentrate seed from other areas either directly beneath it or nearby. The netting, whether hung vertically or laid flat, breaks the current flow and causes small clams to drop out of suspension. This hypothesis is supported by the observation of increased siltation under the netting.

Plastic netting can have a number of beneficial influences and may prove useful in increasing populations of Manila and other clams in both recreational and commercial areas.

ACKNOWLEDGEMENTS

The authors wish to thank Mr. Brian Johnson, the Business Manager for the Squaxin Island Indian Tribe, who was instrumental in establishing the study and providing sites and equipment, and to Mr. Rick Harris and Mr. Jack Rensel, the biologists for the tribe who provided invaluable assistance in the planning and field work. Thanks is also extended to Drs. Roy Nakatani and Jack Matches for their review of the original manuscript, and Dr. Steve Mathews and Mr. Mark Caldwell for their suggestions concerning statistical analysis of the data.

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LITERATURE CITED

Chew, K. K. 1975. Prospects for successful Manila clam seeding. Washington Sea Grant Publication No. WSG-TA-75-15. 16pp.

Gaumer, T. F. 1976. Methods of supplementing

clam and abalone production. July 1, 1975-June 30, 1976. Fish Commission of Oregon Proc. Rept. 35pp.

Holland, D. A. and K. K. Chew. 1973. Reproductive cycle of the Manila clam (*Venerupis japonica*) from Hood Canal, Washington. Proc. National Shellfish. Assn. 64:53-58.

Jones, C. R. 1974. Initial mortality and growth of hatchery-reared Manila clams, *Venerupis japonica*, planted in Puget Sound, Washington, beaches. M.S. Thesis, University of Washington, Seattle, Washington. 90pp.

Miller, M. B., K. K. Chew, C. R. Jones, L. Goodwin, and C. D. Magoon. 1978. Manila clam seeding as an approach to clam population enhancement. Washington Sea Grant Publication WSG-78-2.

Quayle, D. B. and N. Bourne. 1973. The clam fishery of British Columbia. Journal Fish. Res. Bd. Can. Bulletin #179. 71 pp.

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RAZOR CLAM, SILIQUA PATULA DIXON, BREEDING AND RECRUITMENT AT MASSET, BRITISH COLUMBIA

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ABSTRACT

Razor clams have a scattered distribution in British Columbia but occur in sufficient density on a 40 km stretch of surf-swept beach along the northeast coast of Graham Island to support a small fishery. Time of spawning of this clam population has been determined by histological examination of gonads, and recruitment has been monitored by screening plots at monthly intervals in some years, and yearly in the late fall. Gonads of adults from the intertidal beach are ripe in late spring but major spawning of this population does not occur until July to September. Juvenile clams (2 mm shell length) first appear on Masset beaches in July. Recruitment declined steadily from a density of 171 clams per m² in 1966 to 13 per m² in 1972 and has remained at 10 to 15 clams per m² since then. Recruitment has been consistently higher on North Beach (the most easterly section of beach) than on South Beach (the most westerly section of beach). Juvenile clams are distributed fairly evenly horizontally along the 14.5 km of North Beach but recruitment is consistently higher near the low tide level. Environmental factors affecting breeding and recruitment have been examined but do not appear to provide an adequate explanation for the decline in recruitment.

INTRODUCTION

Razor clams are found in the Northeast Pacific region from Pismo Beach, California to the Aleutian Islands (Weymouth and McMillin, 1930) and occur in sufficient populations to support fisheries in several localities: Oregon (Hirschhorn, 1962), Washington (Tegelberg, 1964), British Columbia (Bourne, 1969), and Alaska (Nickerson, 1975) (Figure 1). In British Columbia there are two centers of concentration: Long Beach on the west coast of Vancouver Island, and near Masset in the Queen Charlotte Islands. The razor clam population at Long Beach is small and of importance only to the recreational fishery. The population at Masset is larger, and has supported a small fishery since 1924. Landings have fluctuated over the years; a maximum of 757 metric tons was recorded in 1925 (Figure 2).

Previous studies at Masset assessed razor clam population size and structure, determined if fluctuations in landings were due to populations changes or availability of effort, observed the time of spawning and measured recruitment (McLean-Fraser, 1930; Neave, 1948; Bourne, 1969; Bourne and Quayle, 1970). The present report provides additional information on time of spawning, time of year when juvenile clams are first observed on beaches and fluctuations in recruitment over a period of 12 years.

Description of beaches

The Masset beaches are on the northeast coast of Graham Island, Queen Charlotte Islands, and

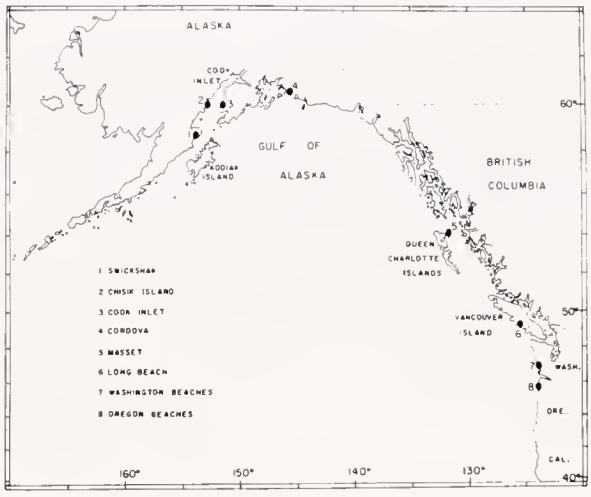

FIGURE 1. *Northeast Pacific Ocean showing the location of major razor clam beaches.*

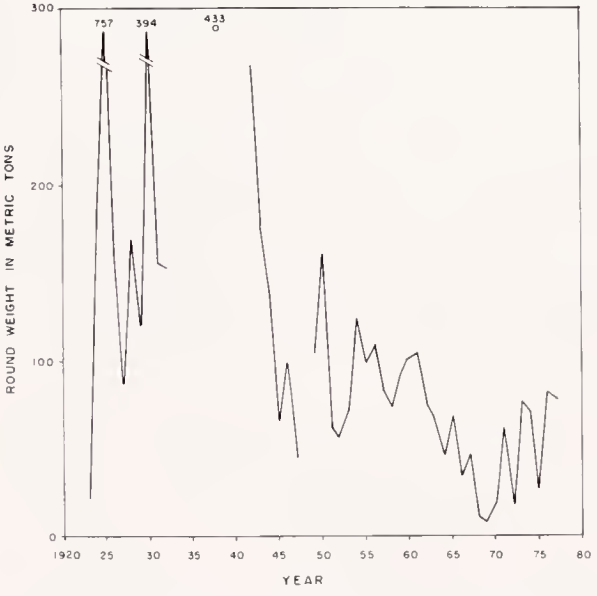

FIGURE 2. *Razor clam landings in metric tons round weight, from Masset, British Columbia, 1924-1977.*

extend from Masset to Rose Spit, a distance of 40 km (Figure 3). Not all 40 km of beach have commercially exploitable populations of razor clams. The beach from Masset to Skonun Point is rarely dug since it is not productive. Ths remaining area is divided into three sections: South Beach extends from Skonun Point to Yakan Point, a distance of 14.5 km, although most digging is done in the 10.5 km section from Sangan River to Yakan Point. Horseshoe Beach extends from Yakan Point to Tow Hill, a distance of 2.5 km. North Beach, the most heavily dug of the three beaches, extends 14.5 km from the Hiellen River to Rose Spit.

North Beach has a maximum width, distance from the lowest low water to the driftwood line, of about 370 m near the Hiellen River and narrows to approximately 300 m near Rose Spit. Maximum tidal range over the Masset Beaches is about 5.3 m and the mid-intertidal beach is about the 2.5 m tidal level. The beach is mostly fine sand.

Horseshoe Beach has a low water terrace that is exposed at low tide, then rises steeply into a berm. Maximum width of the low terrace is about 120 m. The low water terrace has more coarse sand to fine gravel than North Beach, the berm being mostly coarse gravel and small stones. Razor clams only occur in the low water terrace.

South Beach has a maximum width of 350 m. The beach has considerable coarse sand to fine gravel, more so than Horseshoe Beach. Mid- intertidal beach is at about the 2.5 m tidal level.

Time of spawning

Time of spawning was studied on two occasions: February to September, 1966 and September 1969 to August 1970. In the first series, samples of 25 adult clams were collected randomly in February and monthly from May to September from the lower half of North Beach. In the second series, samples of 25 clams were collected at

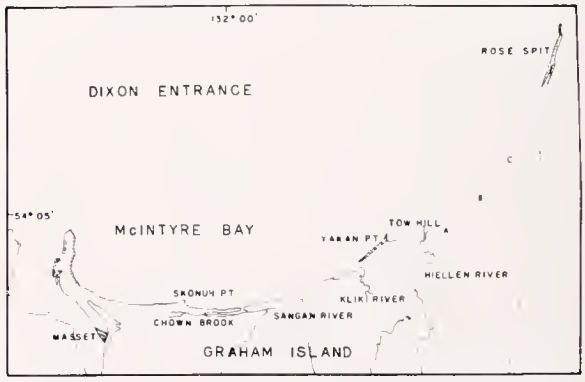

FIGURE 3. *Northeast part of Graham Island, Queen Charlotte Islands, showing the location of the Masset beaches. The letters A, B, and C indicate the position of the transects on North Beach.*

monthly intervals from the 0.5 m intertidal level at Transect A on North Beach (Figure 3).

In both sampling periods, the lower part of the gonad was removed and preserved in Davidson's solution. Histological slides, stained with haematoxylin-eosin were prepared from 5 micron sections.

Several classification schemes have been used to describe the reproductive cycle in bivalves. In the present study, the main interest was to determine when the gonads were ripe and when spawning occurred. The classification scheme adopted was similar to the one used by Chipperfield (1953) to study the reproductive cycle in mussels, *Mytilus edulis*. The reproductive cycle was divided into five stages which also serve as numerical development factors.

Stage 0: Gonad in neuter or resting stage; no follicles present.

Stage 1: Onset of gametogenesis; follicles developed; spermatids present and oocytes are small.

Stage 2: Follicles well developed and filled with unripe ova and sperm.

Stage 3: Ova and sperm ripe and capable of fertilization; sperm activated by sea water.

Recently spent stage: Spawning has occurred; most follicles empty; a few relict ova and sperm present only.

An index or mean stage of gonad development is obtained by taking the sum of individuals falling into each stage, multiplying this by the numerical development factor and dividing this product by the number of animals in the sample. A weighted mean state of development is obtained which has a minimum value of zero if all the animals are in the resting stage and a maximum value of 3.0 when the entire sample is sexually mature.

In February 1966, gonads of both male and female clams were in stage 2 (developing), but had developed to stage 3 by May (Table 1). No spawning was detected in either the May or June samples. In July, many of the clams had spawned. Spawned-out clams were dominant in the August and September samples.

In the 1969-1970 study, clams were spawned out or in stage 1 in September. In October and November, gonads were beginning to refill and continued to fill from January to April, 1970. In June the gonads were ripe and remained in this stage through July, but no spawning was observed. Most of the razor clams in the August sample were spawned out.

TABLE 1. *Stage of gonadal development of razor clams at Masset, British Columbia, after the classification system of Chipperfield (1953).*

	Year		
	1966	1969	1970
J			2.0
F	2.0		
M			3.0
A			2.3
M	3.0		3.0
J	3.0		3.0
J	2.2 sp		3.0 sp
A	sp		1.7 sp
S	sp	sp	
O		2.4	
N		1.7 sp	
D			

Results of this study indicate that from October to January, razor clams on Masset beaches are recovering from spawning, and initial gametogenesis is taking place. From February to April, gonads are ripening and are ripe in May and June. Some minor spawning may occur as early as June, but large-scale spawning of the population does not take place until July to September.

Considerable variation has been reported in the time of spawning in razor clam populations in the Northeast Pacific. Hirschhorn (1962) reported spawning of razor clams on Clatsop beaches in Oregon usually occurred in late May or early June. Weymouth et al. (1925) found spawning on Washington beaches in late May and early June. Tegelberg (personal communication) found juvenile clams usually first appeared on Washington State beaches in late summer, indicating spawning is in late spring. However, juvenile clams have been observed as early as May and as late as October. The unusually abundant 1966 set apparently resulted from an April spawning (Tegelberg and Magoon, 1969). Nickerson (1975) in his extensive study of Alaskan razor clam populations, found major spawning of the Cordova population began in July and extended through to September, although minor spawning

may have occurred in May and June. He found that the approach to the threshold of spawning was determined by time and temperature. Spawning occurred when 1,350 or more temperature units (cumulative Fahrenheit degrees of the maximum daily deviation ± 32 F. that are observed from January 1 to the onset of spawning) have accumulated. Data are lacking in the present study to determine if razor clams at Masset follow a similar regime.

Recruitment

Recruitment studies were divided into two parts: determination of the time of year when juvenile clams first occur on the beaches, and assessment of fluctuations in recruitment over a period of 12 years.

Methods used in the two studies were similar. Beach screenings followed the methods of Hirschhorn (1962) and Tegelberg (1964). Transects were established on the beaches perpendicular to the water's edge and extended to the high tide line. On North Beach there were three transects: A, B, and C, which were 1, 4 and 7 km east of the Hiellen River, respectively (Figure 3). A single transect was established at the middle of Horseshoe Beach. The single transect on South Beach was just west of the mouth of the Kliki River.

Samples were taken at regular intervals along each transect from the low water line to the mid-intertidal beach. No samples were taken above this point since few razor clams inhabit the upper beach area (Bourne, 1969). In the lower half of the sampling area (lower quarter of the intertidal beach) samples were taken at 7.5 m intervals and in the upper half of the sampling area, at 15 m intervals. Replicate samples were taken at alternate sampling sites in the lower half of the sampling area to determine variability in the sampling method.

Each sample was 0.2 m^2 in area and 25 cm in depth. Samples were washed through a 1.5 mm screen and the small clams removed. Shell length and height of each clam was measured under a dissecting microscope to the nearest 0.1 mm. Clams were grouped into 2 mm length size-classes.

Time of recruitment

Beach screening to determine when juvenile clams first appear on Masset beaches was carried out in two periods: July 1966 to September 1967, and September 1969 to September 1970. In July 1966, samples were taken randomly from the lower half of North Beach at four transects that had been established to estimate adult populations (Bourne, 1969). In the remainder of 1966 and 1967, samples were taken only at Transects A and B. In the 1969 and 1970 work, samples were again taken at only Transects A and B.

Results of the 1966-67 work are given in Figure 4 which shows the size frequency distribution of juvenile clams from all the transects on North

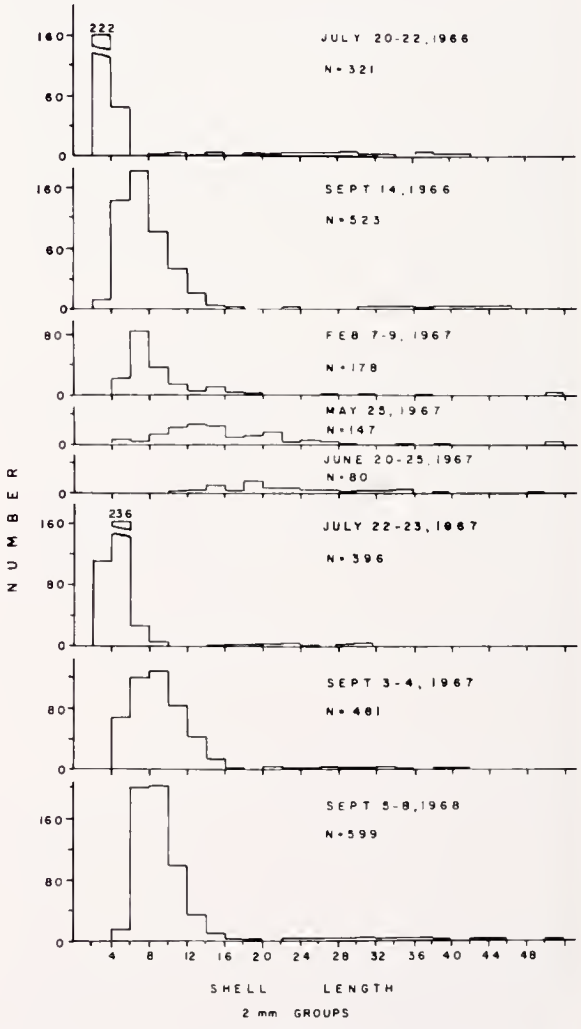

FIGURE 4. *Length frequencies of juvenile razor clams in 2 mm groups collected from Transects on North Beach, Masset, 1966-1968.*

Beach for each sampling period. In July 1966, clams of the zero age group measured 2-6 mm shell length; modal size was 2-4 mm. By September these clams had increased in shell length to 4-10 mm, modal size 6-8 mm. Little growth occurred by February, 1967 and modal size remained at 6-8 mm. In May, clams had a modal shell length of 12-14 mm. By June it was 18-20 mm, but numbers had decreased significantly. The decrease in numbers may be due to selectivity in sampling but more likely to natural mortality.

In July 1967, a new zero age year-class was found. Numbers were large and modal size was 4-6 shell length, 2 mm larger than the modal shell length of zero year-class clams in July of the previous year. By September, modal size had increased to 8-10 mm. A single sample taken in September 1968 showed another zero age year-class with modal shell length 6-10 mm.

From September 1969 to September 1970, a similar pattern of recruitment was evident (Figure 5). Again the size frequency distribution of juvenile clams from both transects on North Beach for each sampling period is shown in the figure. The zero year-class clams had a modal shell length of 8-10 mm in September 1969. These clams showed little growth until the spring of 1970. In August 1970, a new zero age year-class appeared with modal size 8-10 mm. Modal shell length of this year-class was still 8-10 mm in September 1970.

Recruitment of juvenile razor clams 2 mm and larger in shell length occurs annually at Masset during July and August.

Tegelberg (1964) found that major recruitment of juvenile razor clams on Washington State beaches usually occurred in late summer or early fall and the year-class entered the fishery the following year. He reported heavy recruitment of juvenile clams may occur as early as May or as late as October.

At Masset, major spawning of the intertidal razor clam population on North Beach does not occur until July to September. Larval razor clams have not been identified in plankton samples at Masset, but Breese (personal communication) found the larval period in laboratory cultures was about 30 days at 14 C. Thus, settlement from this major spawning at Masset would not be expected until late August to October when spat would probably measure 250-300 microns.

Recruitment of juvenile razor clams at Masset occurs at the same time or slightly before major spawning of the intertidal population, which raises the question as to the source of these juvenile clams.

One possible explanation for recruitment of juvenile clams in July and August is that they come from minor spawnings earlier in the year.

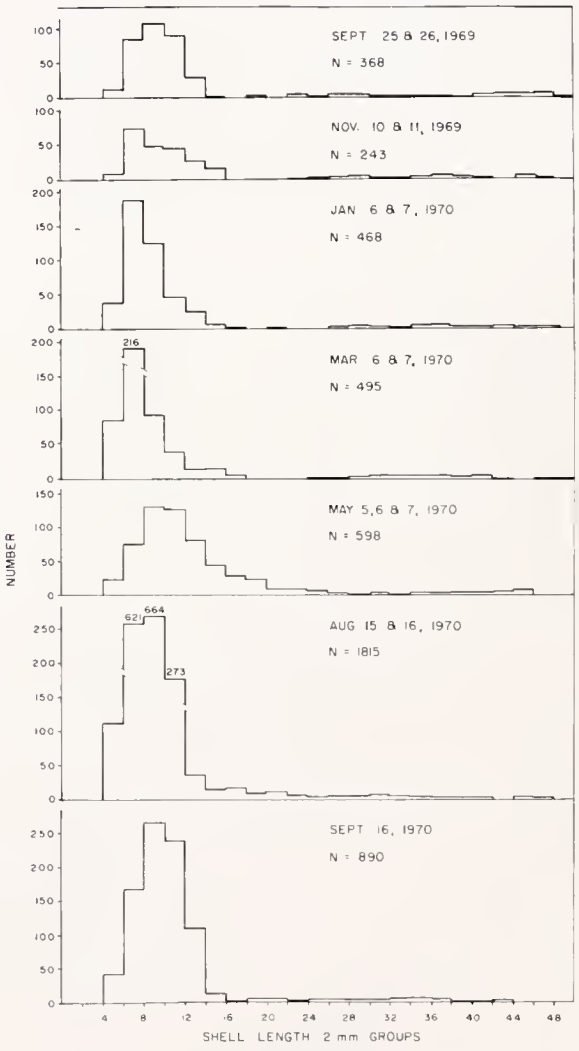

FIGURE 5. *Length frequencies of juvenile razor clams in 2 mm groups collected from two Transects, A and B, on North Beach, Masset, 1969-1970.*

Adults are ripe in May and minor spawning may occur then. Tegelberg (personal communication) found some recruitment in almost every month of the year on Washington State beaches and believes spawning may occur over a long period of time. Larvae from early May spawnings at Masset could settle about the end of the month and spat might attain a length of 2-6 mm in July since this is a period of optimum growth (Figures 4 and 5). However, these early spawnings would be minor and probably would not contribute so dominantly and so consistently to annual recruitment. Further, juvenile clams found in July-August were the major and indeed the only recruitment pulse observed during the year. Populations of small clams decreased in numbers after August. If this recruitment resulted from minor spawnings then one must conclude the major spawning of July-September contributes virtually nothing to recruitment.

Another possible explanation for recruitment of juvenile clams in July and August is that they come from spawnings of populations other than the intertidal one on North Beach, e.g. another area or the subtidal population. Razor clams have been reported from some small beaches west of Masset but the populations are small and it is unlikely that they would contribute significantly to recruitment on North Beach. McLean-Fraser (1930) reported that spawning started slightly earlier on South Beach and was progressively later eastward towards Rose Spit, but the difference in timing between the two areas was only a matter of days. Razor clams are found subtidally off North and South beaches, but the extent of the population is unknown. Regular monthly histological examination of gonads of this subtidal population would indicate if significant spawning occurs there before the major spawning of the intertidal population. Unfortunately such data are lacking.

A third explanation for the occurrence of juvenile clams in July and August is that they come from the major spawning of the previous year. Spat from the major July-August spawning would settle some time from late August to October at a size of 250-300 microns and overwinter under 2 mm shell length. They would not be observed in beach screenings during the winter since the method is selective for clams 4-25 mm shell length. In the spring, they would grow quickly and attain a shell length of 2-6 mm by July. Heavy mortalities could occur to overwintering spat since severe winter storms can cause extensive damage to exposed beaches. However, the Masset beaches are in the lee of southwesterly winds and are protected from the full force of winter storms.

Further studies are needed to determine if razor clams overwinter as spat on Masset beaches. Frequent plankton sampling might show the time of peak abundance of razor clam larvae and give an indication of when settlement occurs. Microscopic examination of the surface sand during the late fall and winter could show if clams 1 mm and less in length are present during that period. Samples should be taken from both the intertidal and subtidal regions since spat may overwinter in the subtidal region and be relocated to the intertidal area in spring.

Recruitment 1966-1977. Beach screenings to assess annual recruitment of juvenile clams were undertaken from 1966 to 1977. Studies included a comparison of recruitment on the three beaches and an assessment of density distribution of juvenile clams on different areas and at different tidal levels of North Beach.

The previous part of this work showed juvenile clams were recruited by September, hence annual screenings were done in the fall. From 1966 to 1970, inclusive, sampling was done in September. From 1971 to 1977, inclusive, sampling was done in November. In 1969, samples were taken in both September and November.

Previous studies showed denser adult populations closer to the low water line than higher on the intertidal beach (Bourne, 1969). To determine if recruitment followed a similar pattern, each transect was arbitrarily divided into three sections: Section 1 extended from the lowest low water line to the 1 m tidal level; Section 2 from the top of Section 1 to the 1.75 m tidal level; Section 3 from the top of Section 2 to the 2.5 m tidal level which was at the mid-intertidal beach. The width of Section 1 varied depending on tide and amount of surf; Sections 2 and 3 were 60 m.

All results are expressed as clams per m^2.

Recruitment was consistently higher on North Beach than on South Beach (Figure 6). Few

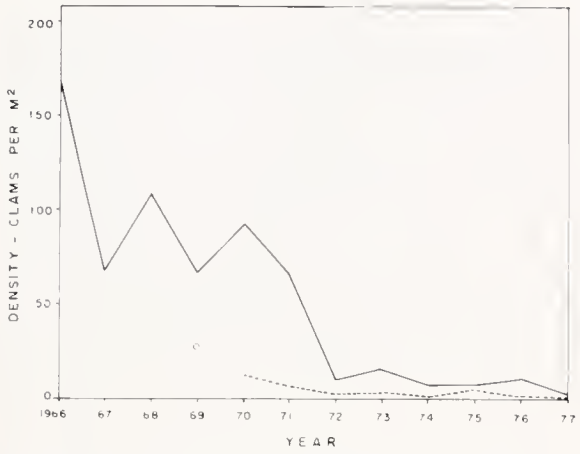

FIGURE 6. *Density of juvenile razor clams collected on North and South Beaches, 1966-1977. Solid line North Beach, dashed line South Beach. Circle in 1969 is the November sample; September sample is on the line.*

samples were taken on Horseshoe Beach, but they show that recruitment was intermediate to that on North and South beaches. This agrees with previous studies that showed populations were largest and growth fastest on North Beach (Bourne, 1969).

Recruitment of juvenile clams declined gradually on North Beach from 1966 to 1971, then dropped suddenly and has remained around 10-15 clams per m^2. Recruitment on South Beach was observed to be low, but decreased still further after 1970. From 1966 to 1970 inclusive, sampling was conducted in September and in the remaining years in November. In 1969 samples were taken in both September and November and numbers were much lower in November than in September. Differences in densities of juvenile clams between the 2 months may be due to movement but more likely to natural mortality. Even when the difference in clam densities between the 2 months is taken into consideration, there was a significant drop in recruitment after 1971, since sampling in that year was in November.

The density of juvenile clams was similar at the three transects, indicating recruitment is fairly general horizontally over North Beach (Figure 7). The decline in intensity of recruitment after 1971 was observed at all three transects.

Highest recruitment in all years occurred in Section 1, the part of the beach closest to the low tide line (Figure 8). Next highest densities were in Section 2, except for one year, 1970. Lowest densities were in Section 3 which is closest to the mid- intertidal beach.

Decrease in clam density followed the same pattern in all three sections. There was a gradual decline until 1971 and then a significant decrease in 1972. Since 1972, densities have remained low in all three sections.

The difference in recruitment between North and South beaches agrees with results of previous work (Bourne, 1969; Bourne and Quayle, 1970). The adult population was smaller and growth slower on South Beach than on North Beach. Tegelberg (1964) reported a similar situation on Washington State beaches. Recruitment was most consistent and growth fastest on Mocrocks Beach,

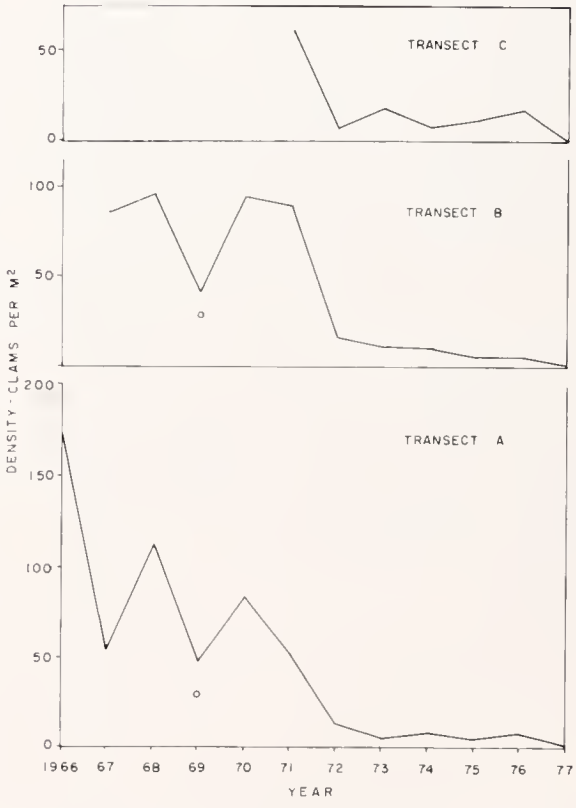

FIGURE 7. *Density of juvenile razor clams collected at the three transects on North Beach, 1966-1977. Circle in 1969 is the November sample; September sample is on the line.*

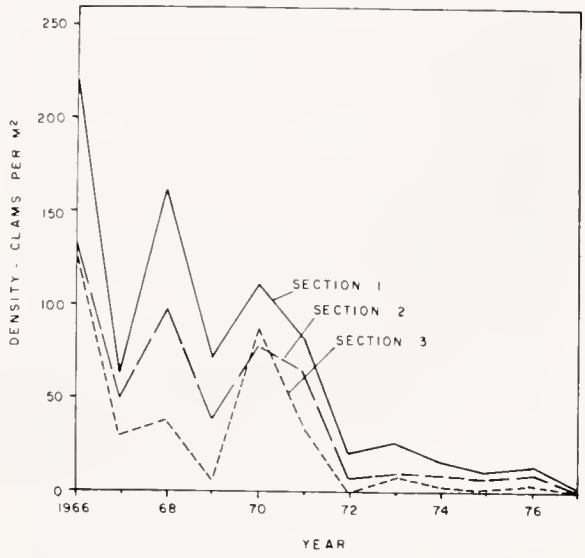

FIGURE 8. *Density of juvenile razor clams by section on North Beach, 1966-1977.*

the most northerly of the four main beaches. He postulated that slower growth on the southern beaches may be due to the greater influence of water from the Columbia River. Salinities are lower on the southern beach (Long Beach), particularly during spring discharge. The sand is coarsest in the south and finest in the north.

A similar situation may exist between North and South beaches at Masset. The sand is much coarser on South Beach than on North Beach. Water coming out of Masset Inlet, particularly during periods of high runoff, probably has a reduced salinity and this may affect South Beach more than North Beach. Although recruitment as measured in this work has been low on South Beach, the beach has supported extensive commercial digging during past years.

Heaviest recruitment in the lowest section agrees with previous results. Densest populations of adults and fastest growth rates were found there (Bourne, 1969). Nickerson (1975) found the density of razor clams at Cordova, Alaska, followed a negative binomial distribution with the mode at lower mean low water. This agrees with our findings. Our results have been grouped into sections, but the area of maximum abundance noted by Nickerson would correspond to our Section 1.

No explanation can be given at this time for the decrease in recruitment since 1971. Even when the difference in sampling dates is taken into consideration, there has been a gradual decline in recruitment since sampling began, followed by a sharp decline in 1972. An examination of environmental factors does not offer any conclusive explanation for this decline. Wickett (1973, 1978) has shown a steady decline in salinity of surface waters at Station P in the Northeast Pacific during the past 10 years. However, the decreases in salinity are small and it is unlikely they would affect razor clam recruitment at Masset, at least not to the degree observed here. Daily surface water temperature and salinity measurements are taken at Langara Island, off the northwest tip of Graham Island. Although mean monthly surface water temperatures since 1966 have fluctuated around the 30-year mean, there does not appear to be a general trend.

Crean (1967) concluded the dominant feature of the net tidal circulation in Dixon Entrance is a cyclonic vortex centered approximately between Cape Chacon, Prince of Wales Island, Alaska and Rose Spit, which in the period from June to August includes the seaward approaches. There is a net inward flow of water along the southern side of Dixon Entrance which may be enhanced by westerly winds. These oceanographic conditions could affect the distribution of larvae in surface waters, regulate settlement patterns and influence the supply of food as well as causing water coming out of Masset Inlet to have a greater effect on South Beach than on North Beach. There may have been significant changes in the position of the vortex which affected settlement patterns recently, but the data are lacking.

Another factor that might affect recruitment is the severity of storms. The Masset beaches lie in the lee of southeasterly winds and hence are protected from the full force of winter storms. However, they are open to westerly winds, and westerly storms at particular times could affect settlement and produce heavy natural mortalities. This could be of significance if juvenile clams over-winter at under 2 mm shell length.

SUMMARY

The period of major spawning of razor clams at Masset is from July to September.

Juvenile razor clams, 2 mm and larger in shell

length, are first observed on the Masset beaches in July and may come from the major spawning of the previous year.

Recruitment is consistently heavier on North Beach than on South Beach.

Recruitment is relatively even horizontally over North Beach, but consistently greater close to the low tide level.

Recruitment of juvenile clams declined gradually from 1966 to 1971, then decreased sharply and has remained around 10-15 clams per m^2 since then. No conclusive explanation can be given for this decline.

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LITERATURE CITED

Bourne, N. 1969. Populations studies on the razor clam at Masset, British Columbia. Fish. Res. Board Can. Tech. Rep. 118. 24 p.

Bourne, N., and D. B. Quayle. 1970. Breeding and growth of razor clams in British Columbia. Fish. Res. Board Can. Tech. Rep. 232. 42 p.

Chipperfield, P.N.J. 1953. Observations on the breeding and settlement of *Mytilus edulis* (L) in British waters. J. Mar. Biol. Ass. U.K. 32: 449-476.

Crean, P.B. 1967. Physical oceanography of Dixon Entrance, British Columbia. Fish. Res. Board Can. Bull. 156. 66 p.

Hirschhorn, George. 1962. Growth and mortality rates of the razor clam *(Siliqua patula)* on Clatsop beaches, Oregon. Fish. Comm. of Oregon, Contrib. No. 27. 55 p.

McLean-Fraser, C. 1930. The razor clams, *Siliqua patula* (Dixon), of Graham Island, Queen Charlotte Islands group. Trans. Roy. Soc. Canada, Series 3, 24 (Sect. 5): 141-154.

Neave, Ferris. 1948. Records of clam production. Province of British Columbia, Provincial Dept. of Fisheries Rep. for year ending 1947: 87-89,

Nickerson, R. G. 1975. A critical analysis of some razor clam *(Siliqua patula,* Dixon) populations in Alaska. Alaska Dept. of Fish and Game Pub. 294 p.

Tegelberg, H. C. 1964. Growth and ring formation of Washington razor clams. Wash. Dept. Fish. Fisheries Research Paper 2, No. 3: 69-103.

Tegelberg, H. C., and C. D. Magoon. 1969. Growth, survival and some effects of a dense razor clam set in Washington. Proc. Nat. Shellfish. Assoc., 59: 126-135.

Weymouth, F. W., and H. C. McMillin. 1930. Relative growth and mortality of the Pacific razor clam *(Siliqua patula,* Dixon) and their bearing on the commercial fishery. U.S. Bureau Fish., Bull. 46: 543-567.

Wickett, W. Percy. 1973. Our changing ocean environment. Fish. Res. Board Can. Pac. Biol. Stn. Circ. 94. 24 p.

Wickett, W. Percy, and A. Ballantyne. 1978. Graphs of surface salinity at nine northeast Pacific stations: Langara Island, Triple Island, Bonilla Island, Cape St. James, McInnes Island, Pine Island, Kairn Island, Amphitrite Point, and Ocean Station P. Fish. Mar. Serv. Data Rep. 95.

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COMPARATIVE SURVIVAL AND GROWTH RATES OF HARD CLAMS *MERCENARIA MERCENARIA*, PLANTED IN TRAYS SUBTIDALLY AND INTERTIDALLY AT VARYING DENSITIES IN A SOUTH CAROLINA ESTUARY [1], [2]

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ABSTRACT

Seed hard clams, Mercenaria mercenaria, *were planted in protective trays subtidally and intertidally at densities of 290, 869, and 1,159/m². Densities were maintained throughout the experiment. The average size of clams remained similar for the first 7 months of the experiment (May through December 1975). Thereafter, clams at a density of 290/m² grew faster than the others. Clams at a density of 290/m² attained an average length of about 44 mm 19 months after planting. Clams at the highest density took approximately 12 months longer to attain that size. Survival of clams at 290/m² was significantly lower than that of clams planted at higher densities. A clam mariculture strategy for South Carolina is presented.*

INTRODUCTION

In recent years harvests of clams in South Carolina have increased dramatically due to the development of an experimental clam fishery in the Santee River estuary. Record yields from this fishery and increasing prices for clams has stimulated interest in clams in South Carolina. The South Carolina Wildlife and Marine Resources Department has undertaken projects to investigate the feasibility of clam culture and of expanding the native clam fishery. Eldridge et al. (1976) reported that clams in intertidal areas could be reared to commercial size within two years of planting. The study also showed a significant difference in growth rates apparently depending upon the level of planting site in the intertidal zone.

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[2] Contribution No. 1642 from South Carolina Agricultural Experiment Station.

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The present study, a cooperative effort with Clemson University, was designed to determine if clam growth differed significantly between intertidal and subtidal locations and if population density affected clam growth and survival. Additional objectives, which will be reported later, included determination of the onset of sexual maturity, the reproductive cycle of cultured clams, detailed growth relationships, and bioenergetic characteristics of clams. The latter objective was directed particularly to C:N ratios and how they might be affected by crowding, spawning, and changes in environmental conditions (e.g. water temperature).

MATERIALS AND METHODS

Seed clams, mean shell length = 13.01 mm, were obtained from Coastal Zone Resources Corporation of North Carolina. These were planted in May 1975 in protected oyster trays (118 x 61 x 14 cm) containing approximately 14 cm of natural sediment. Trays were constructed of ¼ inch iron bars covered with 9 mm mesh plastic cloth (0.1 m^3 basket compartment). Trays were lined with fiberglass insect screen to retain sediment and fitted with 9 mm plastic cloth covers. Trays were placed in a sheltered area near Clark Sound, South Carolina (Lat. 32°42'5" N, Long. 79°52'2" W) (Figure 1). This area is characterized by mostly sand (20-30% silt-clay) and a salinity of 25-30°/$_{oo}$ at low tide (Table 1).

A total of 20 trays were used in two experimental series, 10 trays located subtidally and 10 intertidally. Three density levels (200, 600, and 800 clams/tray corresponding to 290, 869, and 1,159 clams/m^2) were tested at each location with four trays of 200 clams and three of 600 and 800 clams, respectively. A total of 5,000 clams were planted at each location.

Trays were sampled 20 times from May 1975 to May 1978 (Table 1). Initially, trays were sampled monthly changing to quarterly sampling when mortality was negligible. Each tray was seived and the number of live and dead clams was determined for each observation period. Potential predators occurring in the experimental trays were collected (Whetstone and Eversole, 1978). A random sample of 35 live clams was measured for shell length from each tray (105 or 140 clams/density/location). Clams representative of the size distribution of a tray, usually five clams each density and tidal location, were selected and sacrificed at each period. At the end of the experiment a random sample of 200 clams was measured from each tray. Sacrificed clams were fixed in 10% neutral formalin and stored therein for bioenergetic,

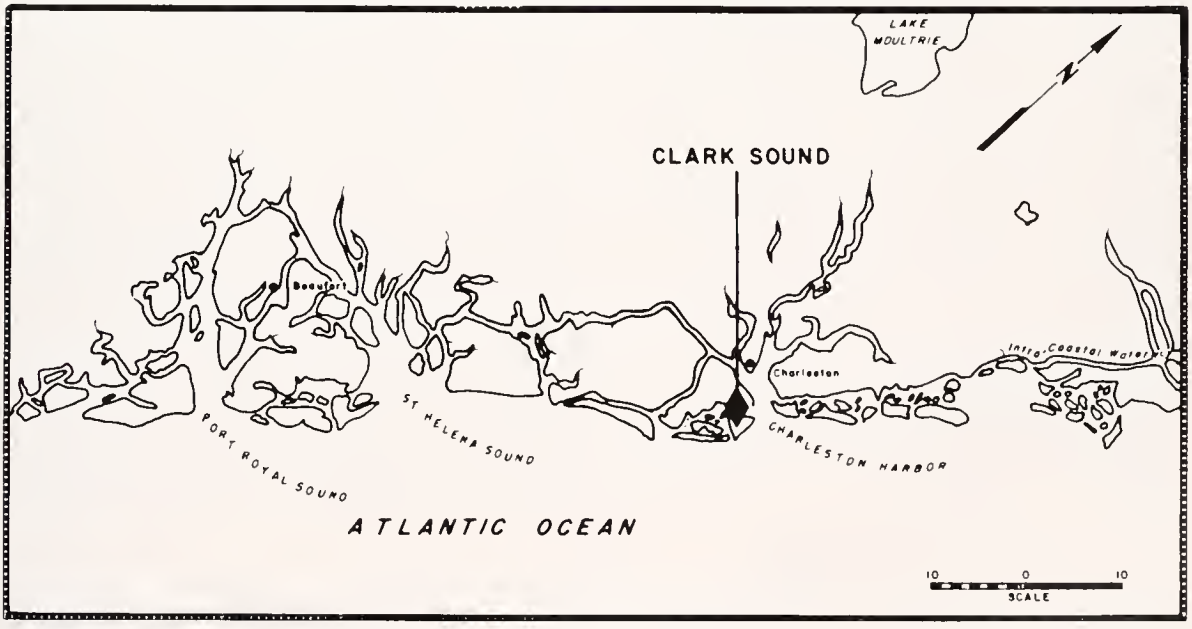

FIGURE 1. *Location of experimental hard clam site in South Carolina.*

TABLE 1. *Summary of temperatures and salinities at Clark Sound, South Carolina. Maximum and minimum water temperatures are recorded as extremes experienced by the subtidal population for the sampling interval.*

	TEMPERATURES (°C)				
SAMPLING DATE	AIR	WATER	MAXIMUM WATER	MINIMUM WATER	SALINITY (°/₀₀)
June 1975	28.0	26.5	34.5	25.6	30
July 1975	29.0	27.7	30.0	26.7	30
August 1975	28.5	28.6	33.4	26.1	27
September 1975	30.0	29.0	32.2	27.2	29
October 1975	23.8	22.5	33.4	22.2	27
November 1975	25.2	21.8	26.1	18.3	29
December 1975	16.0	15.5	22.2	13.9	27
March 1976	22.0	19.0	20.0	7.2	30
April 1976	20.0	18.0	22.2	13.3	29
May 1976	22.0	21.0	26.1	17.2	25
June 1976	31.0	28.5	28.9	21.7	26
August 1976	28.5	29.0	31.1	24.5	27
September 1976	28.0	25.0	30.0	23.4	27
December 1976	9.5	12.0	26.1	11.1	27
March 1977	21.0	18.0	17.2	5.0	28
June 1977	28.0	21.0	28.9	15.6	29
September 1977	28.0	28.0	28.0	16.7	28
December 1977	16.0	17.0	30.0	15.6	27
March 1978	10.0	16.0	17.2	1.1	27
May 1978	23.0	23.0	27.8	14.4	25

histological, and detailed biometric analysis. Results from these studies will be reported later. Empty shells (dead clams) were collected and measured to provide an estimate of the size frequency distribution of clams lost through mortality during the sample interval.

Initial density levels were maintained throughout the 3 year experimental period. Clams lost through natural mortality and sacrifices were replaced with marked clams of similar size and age. Clams designated as replacement clams were marked with Rustoleum fire hydrant red spray paint and held in other trays.

Two additional trays (400 clams/tray) were placed at each tidal location to assess initial mortality. Mortality one week after planting was approximately 5% and appeared to be caused by mud crabs.

RESULTS AND DISCUSSION

Shell Length of Unmarked vs Marked Clams

Normally, only unmarked clams were sampled and measured from each tray. However, mortalities in 4 of the lowest density trays (3 intertidal and 1 subtidal) were such that marked and unmarked clams were included in growth samples during the latter half of the experiment. It was assumed that the marked clams used to maintain density levels did not grow at significantly different rates than those replaced. To test the assumption, "t" tests were conducted on each sample that included marked and unmarked clams. Thirty-one comparisons were made and in only 2 cases were differences found to be significant. The differences occurred in 2 separate trays and in both cases growth was not significantly different in any other time interval. Thus, the differences appeared to be due to sampling error and we concluded that the assumption that marked and unmarked clams exhibited the same pattern of growth was not violated.

Survival of Clams

Table 2 gives the calculated number of survivors (trays of same densities combined) for in-

TABLE 2. *Survival of hard clam seed,* Mercenaria mercenaria, *planted in protected trays in an intertidal and subtidal zone in Clark Sound, South Carolina (trays of same density combined).*

Number per Square Meter	Original Number In Trays 1975	Survivors June 1975	Survivors July 1975	Survivors August 1975	Survivors September 1975
Intertidal					
290	800	415	297	196	179
869	1,800	1,239	1,101	1,035	950
1,159	2,400	1,544	1,425	1,332	1,211
Total	5,000	3,198	2,823	2,563	2,340
Total survival rate		0.640	0.565	0.513	0.468
Interval survival rate		0.640	0.883	0.908	0.913

	Survivors October 1975	Survivors November 1975	Survivors December 1975	Survivors March 1976
Intertidal				
290	164	160	159	159
869	904	898	889	879
1,159	1,189	1,167	1,156	1,152
Total	2,257	2,225	2,204	2,190
Total survival rate	0.451	0.445	0.441	0.438
Interval survival rate	0.965	0.986	0.991	0.994

	Survivors April 1976	Survivors May 1976	Survivors June 1976	Survivors August 1976
Intertidal				
290	159	158	158	157
869	875	874	873	862
1,159	1,147	1,144	1,143	1,135
Total	2,181	2,176	2,174	2,154
Total survival rate	0.436	0.435	0.435	0.431
Interval survival rate	0.996	0.998	0.999	0.991

	Survivors September 1976	Survivors December 1976	Survivors March 1977	Survivors June 1977
Intertidal				
290	157	155	155	153
869	854	850	849	843
1,159	1,129	1,122	1,121	1,106
Total	2,140	2,127	2,125	2,102
Total survival rate	0.428	0.425	0.425	0.420
Interval survival rate	0.994	0.994	0.999	0.989

	Survivors September 1977	Survivors December 1977	Survivors March 1978	Survivors May 1978
Intertidal				
290	152	151	151	151
869	833	807	801	798
1,159	1,088	1,045	1,036	1,025
Total	2,073	2,003	1,988	1,974
Total survival rate	0.415	0.401	0.398	0.395
Interval survival rate	0.986	0.966	0.993	0.993

Number per Square Meter	Original Number In Trays 1975	Survivors June 1975	Survivors July 1975	Survivors August 1975	Survivors September 1975
Subtidal					
290	800	460	372	361	348
869	1,800	1,303	1,087	1,045	1,009
1,159	2,400	1,989	1,806	1,734	1,656
Total	5,000	3,752	3,265	3,140	3,013
Total survival rate		0.750	0.653	0.628	0.603
Interval survival rate		0.750	0.871	0.962	0.960

	Survivors October 1975	Survivors November 1975	Survivors December 1975	Survivors March 1976
Subtidal				
290	329	259	253	252
869	961	948	941	931
1,159	1,608	1,580	1,565	1,557
Total	2,898	2,787	2,759	2,740
Total survival rate	0.580	0.557	0.552	0.548
Interval survival rate	0.962	0.962	0.990	0.993

	Survivors April 1976	Survivors May 1976	Survivors June 1976	Survivors August 1976
Subtidal				
290	251	250	250	249
869	927	926	924	920
1,159	1,552	1,547	1,541	1,534
Total	2,730	2,723	2,715	2,703
Total survival rate	0.546	0.545	0.543	0.541
Interval survival rate	0.996	0.997	0.997	0.996

	Survivors September 1976	Survivors December 1976	Survivors March 1977	Survivors June 1977
Subtidal				
290	248	247	246	246
869	914	912	908	906
1,159	1,530	1,523	1,512	1,503
Total	2,692	2,682	2,666	2,655
Total survival rate	0.538	0.536	0.533	0.531
Interval survival rate	0.996	0.996	0.994	0.996

	Survivors September 1977	Survivors December 1977	Survivors March 1978	Survivors May 1978
Subtidal				
290	243	241	240	239
869	893	887	881	877
1,159	1,478	1,461	1,445	1,428
Total	2,614	2,589	2,566	2,544
Total survival rate	0.523	0.518	0.513	0.509
Interval survival rate	0.985	0.990	0.991	0.991

tertidal and subtidal locations. The cumulative survival rate for each density was calculated by multiplying the initial number of clams by each successive interval survival rate. Survival was higher at the two higher densities. Survival was also higher in the subtidal location. Survival of clams increased dramatically as shell length of clams increased with the greatest mortality occurring during the first 3 months of the experiment.

A two-way Analysis of Variance (ANOVA) was conducted to confirm differences in survival rates. Survival rates were normalized by an arcsin transformation (Table 3). Differences in survival rates among times, densities, and locations were highly significant ($P<0.01$). Survival was lower in the intertidal zone, perhaps because of the more harsh environment experienced there. Survival rate of clams in the lowest density treatment was significantly lower than in the higher densities.

Calculated survival of clams in this experiment was less than that reported by others (Chestnut, 1952; Carriker, 1956; Gustafson, 1955; Haven and Andrews, 1957; Menzel and Sims, 1964). Eldridge et al. (1976) reported the difference may be due to the smaller size of clams utilized, and the failure of trays to adequately protect clams from predation by crabs. The replacement of clams, especially early in the experiment when clams were smallest, may have contributed also to the higher mortality rate. The survival rate of the highest density ($1,159/m^2$) was comparable to that reported by Eldridge et al. (1976); whereas, survival in the lower two densities were lower. The total calculated survival rate for this entire experiment was 45.18%.

MacKenzie (1977) studied the effect of predation by *Neopanope sayi* and concluded that this crab was an effective predator on hard clams to 7 mm in shell length. Our tray results indicated that crabs, particularly *Panopeus herbstii*, were effective predators on clams less than 16 or 17 mm in

TABLE 3. *Results of two-way analysis of variance test on survival rates (trays of same density combined).*

Source of Variation	d.f.	F value	Probability F
Location	1	1,376	0.0001
Density	2	3,363	0.0001
Density-Location	2	223	0.0001
Block (TIME)	19	97	0.0001
Error	119		

TABLE 4. *Mean total length of clams by location, by density, and by time period (trays of same density combined).*

	INTERTIDAL			SUBTIDAL		
	290	869	1,159	290	869	1,159
May 1975	13.01	13.01	13.01	13.01	13.01	13.01
June 1975	13.86	13.85	14.09	13.65	14.07	14.86
July 1975	14.95	15.58	15.03	14.78	16.61	16.26
August 1975	15.95	17.35	16.69	16.28	17.94	18.80
September 1975	18.62	19.49	18.40	18.87	21.12	20.78
October 1975	21.51	21.56	22.03	21.45	21.92	21.99
November 1975	23.43	23.80	22.98	24.51	24.64	24.31
December 1975	25.33	25.76	24.97	26.88	25.83	26.04
March 1976	31.25	29.96	28.42	32.11	29.70	29.08
April 1976	33.50	32.00	31.34	34.81	34.45	33.16
May 1976	37.37	35.50	35.69	38.47	36.08	35.30
June 1976	38.77	36.86	35.97	40.21	38.83	36.83
August 1976	39.60	37.09	36.15	41.56	37.85	36.65
September 1976	41.12	38.58	36.54	42.21	39.15	37.80
December 1976	44.34	41.00	39.63	44.54	39.24	37.49
March 1977	46.15	41.92	40.20	45.67	41.54	38.47
June 1977	51.56	46.53	44.08	50.58	47.01	44.98
September 1977	52.91	46.73	43.47	52.19	46.19	43.17
December 1977	53.36	47.42	44.14	52.50	46.95	43.67
March 1978	54.77	48.48	45.56	53.93	48.43	43.98
May 1978	56.81	49.28	45.77	57.09	49.85	46.11

length. Also, laboratory experiments revealed that *P. herbstii* of 45 mm carapace width could capture and eat clams 35 mm in length (Whetstone, 1978). *P. herbstii*, the most abundant crab found in trays, probably accounts for the lower survival rate of clams in trays in South Carolina.

Growth of Clams

Table 4 and Figure 2 show the mean sizes of clams by time period, by density, and by location. Small differences in shell length (growth) were observed between locations. Growth was markedly different between densities with the highest growth at the lowest density. Clams maintained at the intermediate density (869/m²) also grew faster than clams at the highest density. A two-way ANOVA confirmed that growth was significantly different among densities ($P<0.01$). Growth between locations was barely non-significant ($P=0.0585$). The density-location interaction term was non-significant (Table 5).

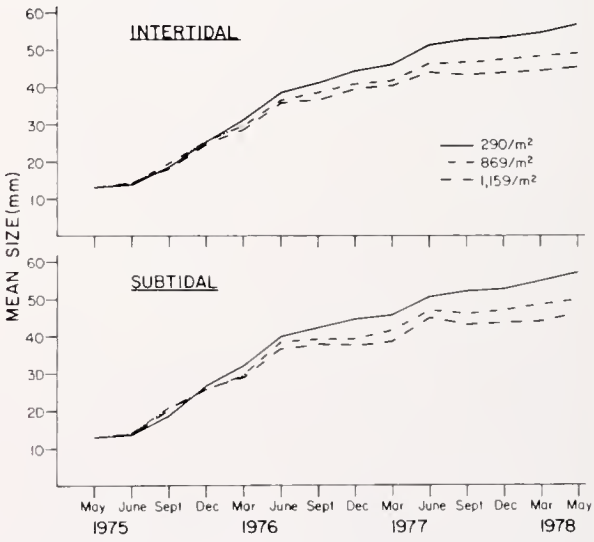

FIGURE 2. *Mean shell length in mm by sampling periods, density, and tidal location for seed hard clams,* Mercenaria mercenaria, *planted in protected trays in South Carolina.*

TABLE 5. *Results of two-way analysis of variance test on growth rates (means of individual trays used in analysis).*

Source of Variation	d.f.	F value	Probability F
Density	2	110.00	0.0001
Location	1	3.60	0.0585
Density-Location	2	0.02	0.983
Block (TIME)	19	701.90	0.0001
Error	375		

Figures 3 and 4 show the incremental increase in mean size of clams during the experiment. During the period of May through December 1975 the increase in shell length combined for all densities averaged 1.8 mm/month. The average increase in shell length declined to 1.3, 0.6, and 0.6 mm/month in 1976, 1977, and 1978, respectively. In 1976, clams at the lowest density (290/m²) grew rapidly. Clams at this density reached commercial size (44-45 mm) by December 1976; clams at the highest density required approximately 12 additional months to achieve the same average size.

Figures 3 and 4 also show the average increase in growth by seasons. Eldridge et al. (1976) reported that growth occurred throughout the year. Similar results were obtained here despite much more severe winter water temperatures. However, best growth was observed during spring and fall when water temperatures and other environmental factors (food availability) may be optimal (Figures 3, 4). Similarly, Menzel (1963) reported that clams grow best in Florida waters in spring and fall.

Interaction Between Growth and Survival

Survival of clams increased markedly between September and December 1975 (Table 2). When clams reached an average length of 16 to 17 mm, the quarterly survival rate approached 95% and the annual survival rate reached 99% when clams reached an average length of 21 to 22 mm. Stated slightly differently, approximately 95% of all mortality was experienced in the first 4 months; 4% in the next three month period; and 1% for the remaining 29 months.

Mariculture Strategy in South Carolina

Experiments in South Carolina indicate that survival of clams is positively correlated with increased average size of clams and cooler water temperatures. Other studies suggest that shell or aggregate substrate and areas without extensive wave action or shifting substrate improve survival of clams (Castagna, 1970; Godwin, 1968). In trays, survival approached 90 to 95% when clams reach 16 to 17 mm in average size. Finally, clams averaging 13 mm in length planted at a density of 290/m² can attain a mean size of 44 mm in about 18 months and 51 mm in 24 months.

The above observations suggest the following clam mariculture strategy for South Carolina.

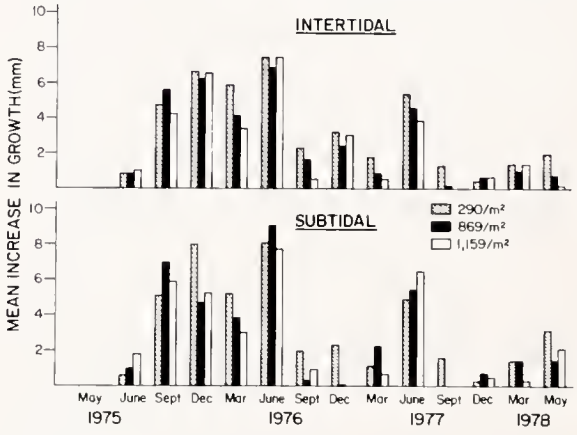

FIGURE 3. *Mean absolute increase in shell length in mm by three month periods, density, and tidal location for seed hard clams planted in protected trays in South Carolina.*

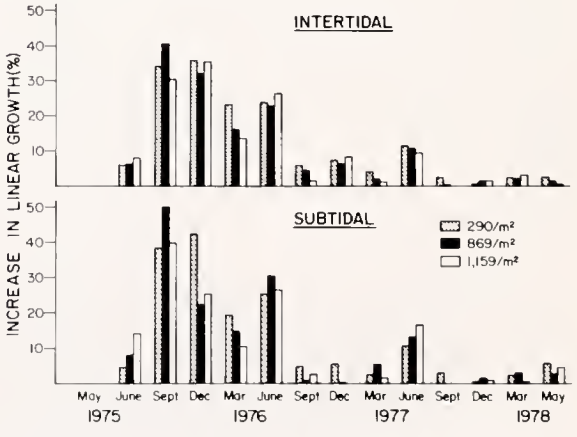

FIGURE 4. *Mean percent increase in shell length in mm by three month periods, density, and tidal location for seed hard clams planted in protected trays in South Carolina.*

First, one should select a suitable habitat, for example, an area which is not exposed to extreme wave action and where clams are presently found. Many small estuarine creeks in South Carolina fulfill this condition. Next, the creek bottom selected should be covered with shells or similar aggregate at approximately one bushel per square meter during the summer months. The following fall, when water temperatures are between 15 and 18C° and declining, clams 12 to 15 mm in average size should be planted at approximately 300/meter^2. Menzel (1971) has suggested planting seed clams at densities ranging between 250 and 500/meter^2. The clams should attain an average size of about 45 mm (commercial little neck size) in early summer of the second year about 18 months following planting. This would correspond to the summer clam bake season, an ideal time for sale of clams. Of course, clams could be held until the following winter when clam prices in South Carolina normally are highest. A constant supply of clams through mariculture operations should make it easier to develop local markets. Finally, shell aggregate may enhance setting of native clams (Walter Godwin, North Carolina Department of Natural Resources and Community Development, Wrightsville Beach, North Carolina) in addition to providing protection; hence total yield may be increased.

The authors feel it would be risky at this time for a private investor to undertake such a project. However, it appears that such a pilot project including an economic feasibility analysis would be an ideal candidate for those governmental programs commissioned to aid or benefit the sea food industry.

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LITERATURE CITED

Carriker, M. R. 1956. Biology and propagation of young hard clams, *Mercenaria mercenaria*. J. Elisha Mitchell Sci. Soc. 72: 57-60.

Castagna, M. 1970. Field experiments testing the use of aggregate covers to protect juvenile clams. Proc. Natl. Shellfish. Assoc. 60: Abstract.

Chestnut, A. F. 1952. Growth rates and movements of hard clams, *Venus mercenaria*. Proc. Gulf and Carib. Fish. Inst. 4th Ann. Session: 49-59.

Eldridge, P. J., W. Waltz, R. C. Gracy, and H. H. Hunt. 1976. Growth and mortality rates of hatchery seed clams, *Mercenaria mercenaria*, in protected trays in waters of South Carolina. Proc. Natl. Shellfish Assoc. 66: 13-20.

Godwin, W. 1968. The growth and survival of planted clams, *Mercenaria mercenaria*, on the Georgia coast. Cont. Series No. 9, Georgia Game and Fish Commission: 16 p.

Gustafson, Alton H. 1955. Growth studies in the quahog *Venus mercenaria*. Proc. Natl. Shellfish. Assoc. 45: 140-150.

Haven, D. and J. D. Andrews. 1957. Survival and growth of *Venus mercenaria*, *Venus campechiensis*, and their hybrids in suspended trays and on natural bottoms. Proc. Natl. Shellfish. Assoc. 47: 43-49.

Mackenzie, C. L., Jr. 1977. Predation on hard clam *(Mercenaria mercenaria)* populations. Trans. Am. Fish. Soc. 106(6): 530-537.

Menzel, R. W. 1963. Seasonal growth of the northern quahog, *Mercenaria mercenaria* and the southern quahog, *M. campechiensis*, in Alligator Harbor, Florida. Proc. Natl. Shellfish. Assoc. 52: 37-46.

Menzel, R. W. and H. W. Sims. 1964. Experimental farming of hard clams, *Mercenaria mercenaria*, in Florida. Proc. Natl. Shellfish. Assoc. 53: 103-109.

Menzel, R. W. 1971. Quahog clams and their possible mariculture. Proc. Second Ann. Workshop World Mariculture Soc: 23-36.

Whetstone, J. M. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs,

Panopeus herbstii. M.Sc. Thesis, Clemson University, Clemson, South Carolina: 58 p.

Whetstone, J. M. and A. G. Eversole. 1978. Predation on hard clams, *Mercenaria mercenaria,* by mud crabs, *Panopeus herbstii.* Proc. Natl. Shellfish. Assoc. 68: 42-48.

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SHELL LENGTH — MEAT WEIGHT RELATIONSHIPS OF OCEAN QUAHOGS, *ARCTICA ISLANDICA*, FROM THE MIDDLE ATLANTIC SHELF

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ABSTRACT

Shell length — drained meat weight relationships were calculated from 2,564 ocean quahogs, Arctica islandica, *taken from the Middle Atlantic shelf during January-February 1978. Significant differences between regression equations were evident among three sub-areas (Southern New England-Long Island, New Jersey, Delmarva). No consistent trends were noted when depth was the major criterion of separation. An increase in relative meat weight for similar sized quahogs along a north to south cline may be indicative of the more stable thermal regime in southern areas, or related to density dependent factors. The overall shell length (L, mm) — meat weight (W, g) regression equation for all Middle Atlantic specimens is ($r = 0.9635$): $\log_e W = -9.589618 + 2.888016 \log_e L$. Allometric growth between shell length and meat weight was confirmed for most areas.*

INTRODUCTION

The ocean quahog, *Arctica islandica* (Linnaeus) is a boreally distributed pelecypod occurring in the North Atlantic Ocean from the Bay of Cadiz (southwest Spain) intermittently to Cape Hatteras (Merrill and Ropes, 1969; Nicol, 1951; Zatsepin and Filatova, 1961). In the Middle Atlantic region off the U.S. coast, commercial concentrations exist in waters from 25 to 61 m deep, although the maximum limits of live quahogs appear to be 15 to 256 m (Merrill and Ropes, 1969). Studies of the life history and in particular the population dynamics of this species are few. Aspects of ocean quahog density and distribution in the Middle Atlantic are reviewed by Merrill and Ropes (1969, 1970) and Parker and McRae (1970). Ropes (1971) calculated total solids and the dry meat-shell length relationship for samples from off Long Island, New York. However, results of systematic quantitative meat yield investigations have not been reported. Objectives of our study were to: (1) calculate shell length-drained meat yield regressions for ocean quahog samples from the Middle Atlantic, (2) investigate the variability associated with the area and depth of capture, and (3) determine the precision of utilizing the computed regression equations to describe empirical data.

METHODS

Ocean quahog samples for length-weight analysis were collected from the Middle Atlantic shelf (Cape Cod to Cape Hatteras) during the

shellfish assessment survey of the R/V DELAWARE II from 4 January to 11 February 1978 (Figure 1). Sampling gear was a commercial-type hydraulic clam dredge with a 1.2 m (48 inch) wide knife and 30 mm spacing between bars of the cage. Stations were selected randomly within area/depth strata; the dredge was towed for 4 minutes at approximately 0.5 m s^{-1} at each site. Ocean quahogs were collected in depths ranging from 13 to 75 m. Subsamples of the catches for length-weight determinations were stratified by 10 mm shell length class (longest dimension). Generally, five intact individuals in each 10 mm length interval (10-19 mm, etc.) were selected at each station; when large numbers of small (<50 mm) or large (>115 mm) quahogs were taken additional samples were retained to increase the total numbers of these sizes. Thus length-weight data should not be considered random with respect to the available population or as unbiased subsamples of the survey catches, but regression equations are probably more accurate over a wider size range of quahogs than those from simple stratified random samples.

Shell dimensions were recorded to the nearest mm, and all soft parts of each quahog shucked into an individual plastic bag. Frozen samples were returned to the laboratory, thawed, and drained on toweling. Total drained meat weight was determined to the nearest 0.1 g. Samples contaminated with sand from the dredging process were rinsed prior to draining.

Linear regression equations were fitted with length and weight data converted to natural logarithms. The form of the length-weight equation was assumed to be:

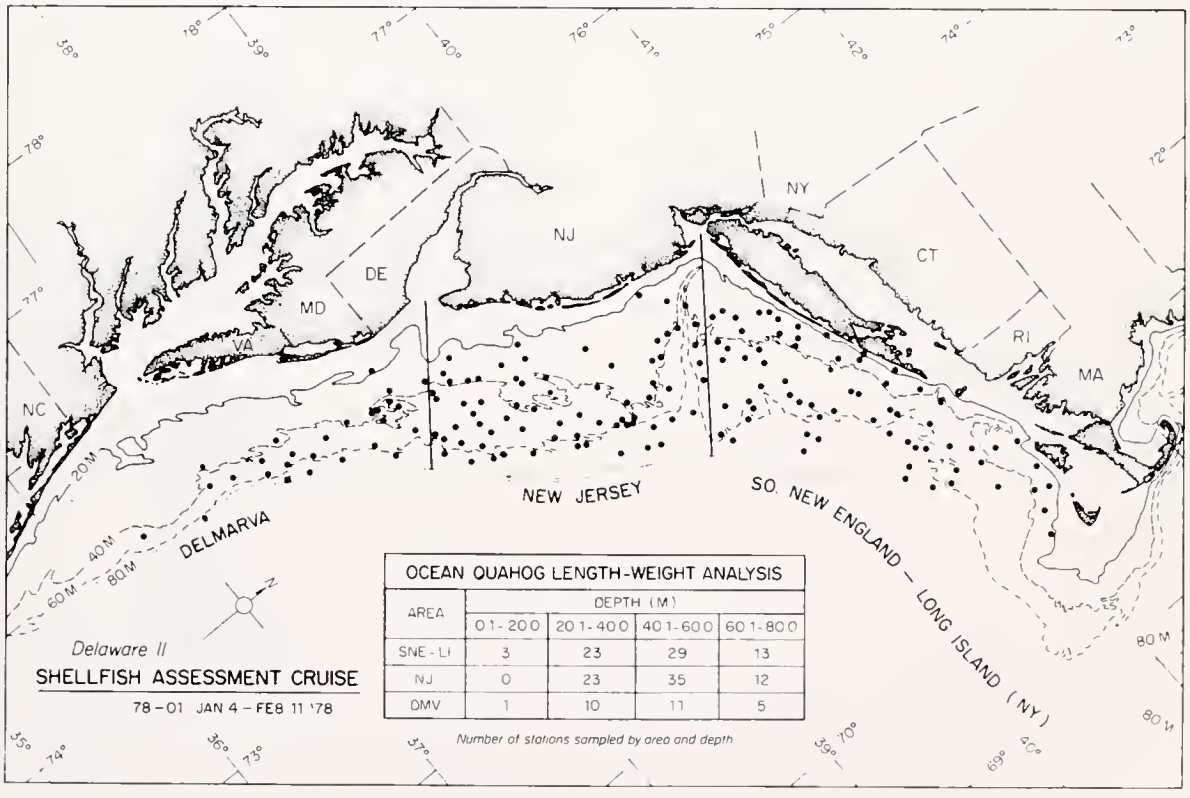
$W = cL^b$

where,

W = drained meat weight (g),

L = shell length (mm),

c and b = coefficients to be estimated from regression.



AREA	DEPTH (M)			
	01-200	201-400	401-600	601-800
SNE-LI	3	23	29	13
NJ	0	23	35	12
DMV	1	10	11	5

FIGURE 1. *Locations of survey stations where ocean quahogs were sampled for length-weight analysis, January-February 1978.*

TABLE 1. *Summary statistics of ocean quahog length-weight data by area caught.*

Area	Shell Length (mm)					Meat Weight (g)			
	n	$\bar{x}$	σ	Min.	Max.	$\bar{x}$	σ	Min.	Max.
Southern New England									
Long Island	1,351	80.73	16.30	17	117	23.77	12.77	0.3	77.6
New Jersey	982	88.87	15.20	30	131	32.39	15.28	1.0	89.4
Delmarva	231	95.76	10.68	59	124	41.02	12.96	7.6	98.6
All Areas	2,564	85.20	16.26	17	131	28.62	14.90	0.3	98.6

Isometric growth (i.e. slope of length-weight regression = 3.0, implying unchanging ratios of linear measurements as the organism grows [Ricker, 1975]) was tested employing Student's t with n-2 degrees of freedom (Steel and Torrie, 1960). Covariance analyses (Snedecor and Cochran, 1967) were conducted to determine the significance of differences between slopes and adjusted means of various length-weight equations. The one-way analysis of covariance computer program BMDP1V was used for all these calculations (Dixon, 1975).

Empirical weights were compared to weights derived from regression equations applied to the shell lengths of samples from several different areas. Empirical weights were totaled for quahogs from the three major areas and for all areas combined. Corresponding total calculated weights were computed by:

$$TCW = \sum_{i=1}^{n} L_i^b \text{ Antilog}_e a$$

where,

TCW = total calculated weight (g),

L_i = shell length of individual, i, in the length frequency, where i = 1, 2, 3, ...n,

b = slope of the length-weight regression specific for the area being studied,

Antilog$_e$ a = antilog$_e$ of the intercept of the length-weight equation used in the analysis (=c).

RESULTS

A total of 192 stations occupied during the cruise yielded ocean quahog catches, of which 165 (86%) were sampled for the length-weight study. Sampling locations were classified by area and 20 m depth interval (Figure 1). Area designations generally correspond to beds frequented by commercial fishermen from the various coastal states, and thus may serve to delimit fisheries. Largest total numbers, and numbers per station were taken from off Southern New England—Long Island with smaller sample sizes to the south reflecting the relative densities of quahogs among the three areas (Merrill and Ropes, 1970; Figure 1; Table 1). The 40.1-60.0 m depth interval accounted for most of the samples from all areas. The total number of quahogs weighed and measured was 2,564.

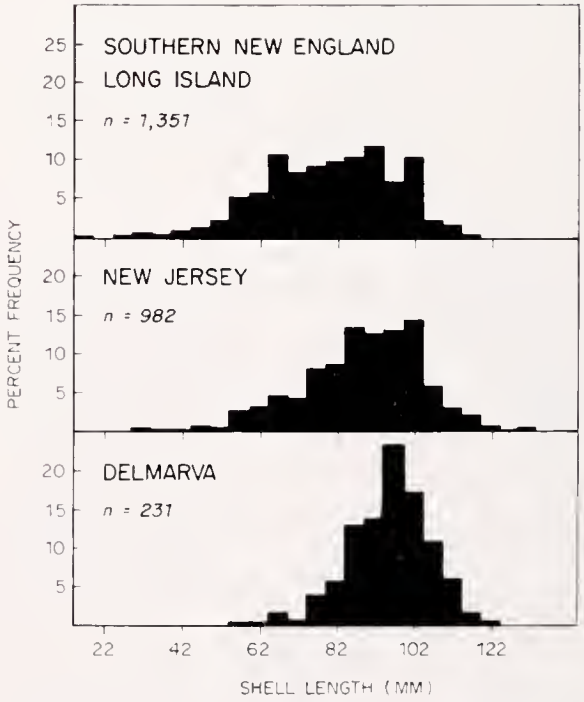


FIGURE 2. *Length frequencies of ocean quahogs sampled for length-weight analysis from the Middle Atlantic shelf.*

Summary Statistics

Statistical summaries of length and weight data for the three major areas, and all data, are presented in Table 1. Smallest mean lengths and weights were sampled from Southern New England—Long Island, with average sizes, as well as modal lengths (Figure 2), increasing to the south. Shell lengths ranged from 17 to 131 mm; the overall average length was 85.20 mm. Meat weights ranged from 0.3 to 98.6 g (mean = 28.62 g). The length frequency from the Delmarva area shows a pronounced mode and the range of sizes is less than in samples from the two northern locations. Samples from Southern New England—Long Island show the most even distribution among size classes. Length-weight regression statistics for each area and the overall equation are expressed in Table 2. Regression equations for individual 20 m depth intervals are given in Murawski et al. (1978). Slopes of regression equations for the major areas were significantly ($P<0.01$) less than 3.0, except for New Jersey. Thus allometric growth functions apply for quahogs from Southern New England—Long Island, Delmarva, and for all data.

Covariance Analyses

Regression equations were tested to determine if significant differences among lines existed due to area and/or depth of capture. In tests among the three major areas, the only significant difference in slopes was between Southern New England—Long Island and New Jersey (Table 3). The slope of the New Jersey equation was significantly greater than that for the Southern New England—Long Island location, indicating the two regression lines were statistically different, with New Jersey quahogs generally containing more meat per unit shell length for the range of lengths considered. Predicted meat weights for New Jersey quahogs smaller than 63 mm were less than corresponding values for Southern New England—Long Island, but this difference may be due to the paucity of these sizes sampled off New Jersey (Figure 2). The adjusted mean of the Delmarva equation was significantly greater than those of the Southern New England—Long Island, and New Jersey equations in paired comparisons (Table 3). Thus separate equations apply for the three areas, and computed meat weights for the range of shell lengths sampled generally increase from Southern New England—Long Island to Delmarva. Results of tests between areas for each of the three 20 m depth strata from 20.1-80.0 m were generally similar to those with all depths combined (Murawski et al., 1978). Differences in regressions due to depth of capture were examined by comparing samples from the three major areas that fell within the four 20 m depth intervals, and by comparing depth groups within each area (Murawski et al., 1978). However, results of these tests revealed no obvious trends in the significance of differences between slopes or adjusted means. Depth of occurrence may directly or indirectly influence the length-weight relationship, but the ef-

TABLE 2. *Statistics describing regression equations between shell length (mm) and drained meat weight (g) for ocean quahogs.*

Area	Regression Statistics				
	Intercept (a)	Slope (b)	S.E. of b	Antilog$_e$ of a	Correlation Coefficient (r)
Southern New England					
Long Island	−9.124283	2.774989	0.0199	0.000108987	0.9670
New Jersey	−9.847183	2.949540	0.0294	0.000052896	0.9546
Delmarva	−9.042313	2.787987	0.0800	0.000118297	0.9172
All Areas	−9.589618	2.888016	0.0159	0.000068436	0.9635

TABLE 3. *Results of covariance analysis of adjusted means and slopes of ocean quahog length-weight regression equations between pairs of areas.*

	Test of Adjusted Means				Test of Slopes		
Areas	Adjusted Mean	F-Ratio	df	Significance Level	F-Ratio	df	Significance Level
Southern New England Long Island vs. New Jersey	NOT APPLICABLE				24.971	1,2329	P<0.01
Southern New England Long Island	3.073						
vs.		139.171	1,1579	P<0.01	0.011	1,1578	n.s.
Delmarva	3.214						
New Jersey	3.387						
vs.		31.256	1,1210	P<0.01	2.691	1,1209	n.s.
Delmarva	3.456						

P<0.01=Significant at 1% level
n.s.=non-significant

fects were not similar among inter-area and intra-area comparisons.

Precision of Computed Weights

Correlation coefficients indicate that from 84 to 94% ($r^2 \cdot 100$) of the variation between shell length and meat weight is accounted for by the regression equations (Table 2). Predicted weights were, however, 0.8, 1.1, 1.3, and 1.4% smaller than the total of empirical weights for Delmarva, New Jersey, Southern New England—Long Island, and all areas, respectively. A slight negative bias is suggested by the fact that all sums of empirical weights were greater than their calculated counterparts, but the magnitude of the differences is quite small. The residuals about the regression lines were plotted against the dependent variable for the three major areas (Figure 3). In all cases the residuals appear normally distributed around 0; no obvious biases appear to exist when the log-linear model is assumed. Thus, the use of our regression equations results in relatively precise approximations of empirical data when converting shell length to meat weight.

DISCUSSION

Results of these analyses indicate meat weights for similar sized quahogs generally increase from Southern New England— Long Island to Delmarva. The consistency of this trend in tests within depth zones and in pooled comparisons suggests differences are probably not merely statistical artifacts. Possible factors affecting the relative condition of quahogs between areas include physical and biological variables such as temperature, salinity, pressure, nutrients, and food supply. The physical oceanography of the Middle Atlantic has been reviewed in detail (Beardsley et al., 1976), and temperature profiles of the area reported by Walford and Wicklund (1968) and Colton and Stoddard (1973) among others. The annual variation in bottom water temperature on the continental shelf within the depth range of ocean quahogs that we sampled is much greater off Long Island and Southern New England (Colton and Stoddard, 1973) than further to the south, as indicated from transects off Cape May, Cape Charles, and Cape Hatteras (Walford and Wicklund, 1968). The seasonal minimum and maximum bottom water temperatures within the sampled range of ocean quahog occurrence are approximately 2°C and 19°C off Southern New England—Long Island, but off Cape Charles are about 7.5° and 17.5°. Stability of the thermal environment may be an important factor governing metabolic processes and ultimately growth, resulting in an in-

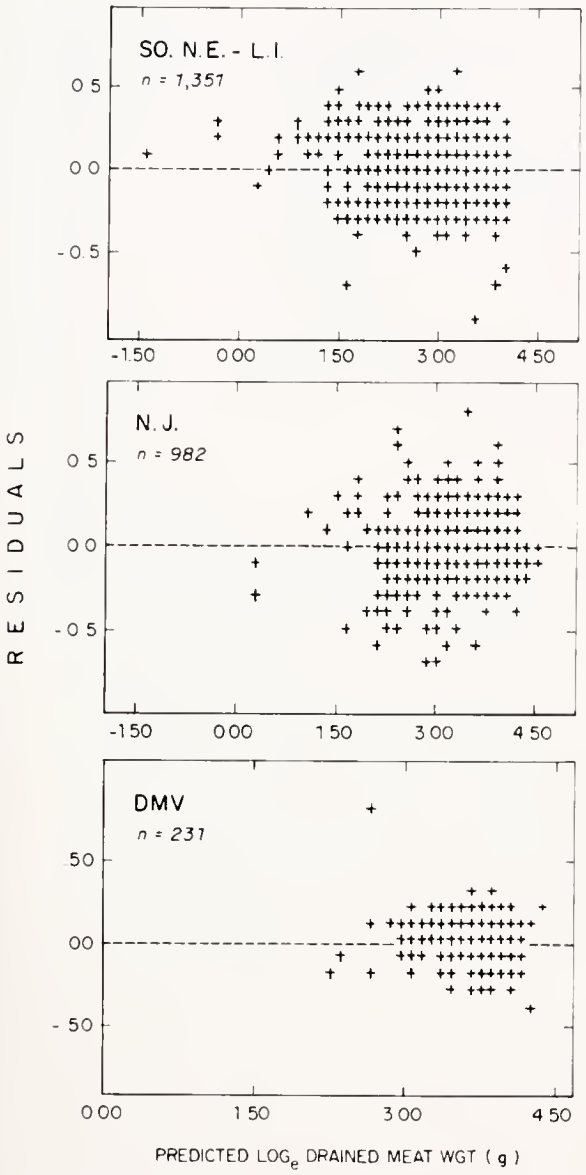


FIGURE 3. *Plots of residual differences between predicted and actual log$_e$ meat weights for ocean quahogs from the Middle Atlantic shelf.*

crease in relative meat yields to the south. Density dependent factors may limit growth in more northern waters, but evidence is only circumstantial (Merrill and Ropes, 1970). The direct effects of environmental variables on growth and condition factors of ocean quahogs are yet to be studied.

Bearse (1976) calculated the length-weight relation from inshore Rhode Island samples (n = 129) as:

$$\log_{10} W = -3.0391 + 2.355 \log_{10} L$$

Computed meat weights for shell lengths he analyzed ($\bar{x}$ = 90.5 mm, σ = 8.3 mm) were slightly greater for Rhode Island than comparable values from our length-weight equations. The higher meat weights off Rhode Island may reflect the greater productivity of these inshore waters, or the season of capture, as his samples were taken in summer and autumn. Further study of ocean quahog lengths and weights from the Middle Atlantic area is necessary to determine if relationships vary significantly on a seasonal or annual basis, or with the state of sexual maturity.

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LITERATURE CITED

Beardsley, R. C., W. C. Boicourt, and D. V. Hansen. 1976. Physical oceanography of the Middle Atlantic Bight. Amer. Soc. Limn., Oceanogr. Proc. Spec. Symp. on the Middle Atlantic Continental Shelf and New York Bight. 2:20-34.

Bearse, D.T. 1976. Density and distribution of the ocean quahog (*Arctica islandica*) in Rhode Island waters relative to various environmental factors. M. S. Thesis, Univ. Rhode Island. 91 pp.

Colton, J. B., and R. R. Stoddard. 1973. Bottom-water temperatures on the continental shelf, Nova Scotia to New Jersey. U.S. Dept. Comm., NOAA Tech. Rpt. NMFS Circ. 376:55 pp.

Dixon, W. J. (ed.) 1975. BMDP Biomedical computer programs. Univ. Calif. Press, Berkeley. 792 pp.

Merrill, A. S., and J. W. Ropes. 1969. The general distribution of the surf clam and ocean quahog. Proc. Nat. Shellfish. Assoc. 59:40-45.

Merrill, A. S., and J. W. Ropes. 1970. The distribution and density of the ocean quahog, *Arctica islandica*. Amer. Malacol. Union Bull. 36:19.

Murawski, S.A., F.M. Serchuk, and M.C. Aelion. 1978. Shell length-meat weight relationships of ocean quahogs, *Arctica islandica*, from the Middle Atlantic shelf. Nat. Mar. Fish. Serv. Woods Hole Lab. Ref. 78-38: 20 pp.

Nicol, D. 1951. Recent species of the veneroid pelecypod *Arctica*. J. Wash. Acad. Sci. 41(3):102-106.

Parker, P.S., and E.D. McRae. 1970. The ocean quahog, *Arctica islandica*, resource of the Northwestern Atlantic. Fishery Industrial Research 6:185-195.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 pp.

Ropes, J. W. 1971. Percentage of solids and length-weight relationship of the ocean quahog. Proc. Nat. Shellfish. Assoc. 61:88-90.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames, 593 pp.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedurss of statistics. McGraw-Hill Book Co., New York, 481 pp.

Walford, L. A., and R. I. Wicklund. 1968. Monthly sea temperature structure from the Florida Keys to Cape Cod. Amer. Geographical Soc. Ser. Atlas Mar. Env. Folio 15.

Zatsepin, V. I., and Z. A. Filatova. 1961. The bivalve mollusc, *Cyprina islandica* (L.), its geographic distribution and role in the communities of benthic fauna. Trans. Inst. Ocean., Acad. Sci. USSR. 46: 201-216 (Translation 74732, Dept. Northern Affairs and National Resources, Ottawa, Canada).

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IMPACTS OF THERMAL ADDITION AND PREDATION ON INTERTIDAL POPULATIONS OF THE BLUE MUSSEL, *MYTILUS EDULIS* L.[1]

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ABSTRACT

Populations of the blue mussel, Mytilus edulis, *were sampled at four locations on nearly vertical intertidal rocky surfaces from 1970 to 1977. One sampling station was adjacent to the thermal discharge weir of the Maine Yankee Atomic Power Co. electric generating plant, and the other stations were located at increasingly greater distances from the plant. Those mussels adjacent to the weir suffered 100% mortality in less than one year after the plant began operation, and recruitment was not observed even though the means of discharge was changed to a diffuser system during the summer of 1975. Mussel populations at the other three stations declined from several thousand per square meter in 1970 to zero in 1977 although mussels continued to pose a fouling problem within the Maine Yankee plant and on nearby floats. Examination of records of organisms impinged upon the traveling screens of the Maine Yankee plant intake structure revealed a dramatic increase in green crabs,* Carcinus maenas, *concurrent with the decline of intertidal mussels. During the fall of 1977, an extensive qualitative examination of the rocky intertidal zone revealed that green crabs of many different sizes were very abundant and that mussels were extremely scarce. Floating docks a few meters away were festooned with mussels of several size groups, including the zero age class. The increase in green crab abundance coincided with an increase in the regional surface sea water annual mean temperature.*

INTRODUCTION

The blue mussel, *Mytilus edulis*, is a circumboreal species ordinarily extending as far south as North Carolina on the Atlantic seaboard of North American (Hutchins, 1947; Wells and Gray, 1960). Surveys by Scattergood and Taylor (1949) document the abundance of this species in Maine's waters. Typically, *M. edulis* lives in extensive intertidal or subtidal beds and coats intertidal rocks and floating objects. Local commercial exploitation of the blue mussel has remained at relatively low levels except during the years of World War II when other sources of protein were scarce. (Dow and Wallace, 1954).

When, in 1968, the Maine Yankee Atomic Power Company began construction of a nuclear-powered electric generating plant (MY) on Bailey Point, Wiscasset, Maine, a team of scientists from the University of Maine at Orono formulated a research program to monitor the flora and fauna of Montsweag Bay, the body of water which would receive the thermal discharge from MY. Most projects of this comprehensive monitoring

[1] Ira C. Darling Center Contribution No. 122

program were started in 1969 or 1970 and were continued at least through 1978.

Some of the data have appeared in the scientific literature, including McCleave and Fried (1974, 1975), Recksiek and McCleave (1973), and Targett and McCleave (1974) on fin fish; Vadas, Keser and Rusanowski (1976), and Vadas, Keser, Rusanowski and Larson (1976) on the effects of thermal loading on flora; Hess et al. (1975) on radionuclides in oysters and sediments; Price et al. (1976) on growth and mortality in rafted oysters; and Lutz and Porter (1977) on growth and mortality in rafted mussels.

The purpose of the present paper is to document the thermal impact MY had on intertidal populations of the blue mussel, *Mytilus edulis*, and to describe a drastic decline in intertidal mussel populations which was not related to power plant operation.

There were several reasons for including the blue mussel as one of the species to be monitored. At the time monitoring studies were initiated, *Mytilus edulis* was extremely abundant on intertidal rocky surfaces all along the coast of Maine. Previous work by Bruce (1926), Richie (1927), Hutchins (1947), Wells and Gray (1960), and Pearce (1969) had demonstrated the thermal sensitivity of this species. The species also was an important recreational resource and it was harvested commercially to a limited degree.

MATERIALS AND METHODS

The Maine Yankee plant (MY) is situated on Bailey Point at the junction of Back River and Montsweag Bay, a portion of the Sheepscot River estuarine system (Figure 1). MY is rated as an 855 MW electric generating plant and utilizes a tertiary loop, pressurized water reactor. The plant uses a once-through cooling system for its condensers, with the intake structure located on the easterly side of Bailey Point. The reactor first went critical in October of 1972 and the plant began producing commercial quantities of electricity later that fall. Until May of 1975, the thermal effluent was discharged into Bailey Cove on the southwesterly side of Bailey Point. Prior to MY operation, Bailey Cove drained at low water. After MY began operation, effluent waters of about 27 m^3/sec were discharged onto tidal flats at

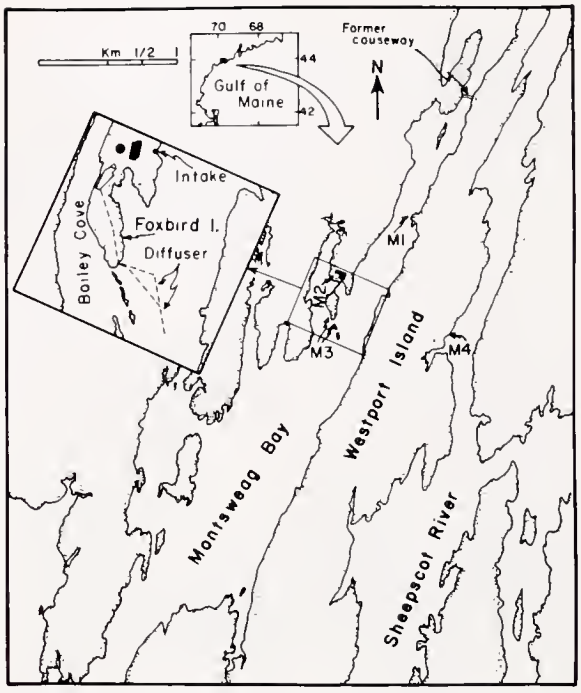

FIGURE 1. *Location of the four intertidal mussel sampling stations, M1-M4, in relation to the Maine Yankee Atomic Power Company plant.*

low water. A dike had been constructed between Bailey Point and Foxbird Island to help prevent the discharge water from reentering the intake structure.

Regulatory agencies required MY to reduce the initial size of the mixing zone from 290 acres (117.4 ha) allowed with the surface discharge and existing physiographic conditions, to a zone of 100 acres (40.5 ha). This was accomplished by construction of a high-rise bridge between the mainland and Westport Island to replace a man-made causeway which was removed during November of 1974. Causeway removal greatly increased tidal flows past MY and permitted compliance. In order to comply with a further decrease in mixing zone size (to 25 acres or 10.1 ha), MY installed a multi-port diffuser system over 300 m in length on the bottom of the channel southeast of Foxbird Island (Figure 1). This mixing zone (now termed a "thermal discharge zone" by the United States Environmental Protection Agency) is designated as that portion of the receiving waters which falls within the delta 2 C isotherm of the

thermal plume 30% or more of the time. The diffuser became operational in late June of 1975. With MY operating at full licensed capacity, this discharge zone now consists of an ovoid volume in approximately the mid-depth region over the diffuser. If the area of this volume were projected onto the bottom it would cover about 13 acres (5 ha). Thus, the thermal impact upon the biota was diminished in stages and the hydrography altered substantially during the study period.

In March, 1970, three mussel sampling stations were selected (Figure 1, M1-M3) to represent three populations of mussels at varying distances from the discharge point. At each site on vertical, or nearly vertical, rocky surfaces about 1.5 m below mean high water (MHW) five 0.1 m^2 quadrats were denuded of all mussels. The mussels from each quadrat were kept separately and were returned to the laboratory where each mussel was measured and the number of each size class counted. Size classes were in increments of 4 mm, e.g., 0-3.9, 4-7.9, etc. The sites were sampled again during summer and late fall. In December of 1970, a fourth mussel station (M4) was added on the east side of Westport Island (Figure 1). These four sites were resampled each spring, summer and fall through November of 1974.

In the spring of 1975, an alternate method of assessing mussel mortality in the intertidal zone was initiated. These studies consisted of placing concrete quadrats, seeded with a known size and number of mussels, in the intertidal zone and photographing them during the spring, summer and fall. Vandalism and other problems yielded inconsistent results. Data from these studies will not be reported here. During November of 1975 and 1976, mussel stations M1 and M2 were sampled as originally described. During November 1977, all four of the original mussel stations were again sampled.

RESULTS AND DISCUSSION

The fall sampling periods provide the longest series of data which can be compared. These data are shown in Figure 2. While Figure 2 shows the absence of mussels since November 1973 at station M2, actually, no living mussels were found when that station was sampled during July 1973. That station is 30 to 45 meters west of the original surface discharge weir. While Price et al. (1976) measured temperatures only at bi-weekly intervals in Bailey Cove about 200 meters downstream from the discharge point, they reported temperatures of 25 C on two occasions prior to July of 1973. Subsequently, Dr. Michael Mazurkiewicz (personal communication) installed continuous temperature recording devices in Bailey Cove and found that temperatures exceeding 30 C existed for short periods (from a few minutes to a few hours). The loss of mussels at M2 was undoubtedly caused by the MY thermal discharge. The decreases in mussel populations at M1, M3, and M4 were strikingly similar. While stations M1 and M4 were beyond the influence of the thermal discharge, station M3 was only 550 to 730 meters from the original discharge point.

Lutz and Porter (1977) studied growth and survival of *M. edulis* suspended from rafts located at various distances from the MY discharge. Recruitment was measured by counting mussels that attached to ropes hung from the rafts. They reported a positive correlation of survival with linear distance from the discharge point. In the

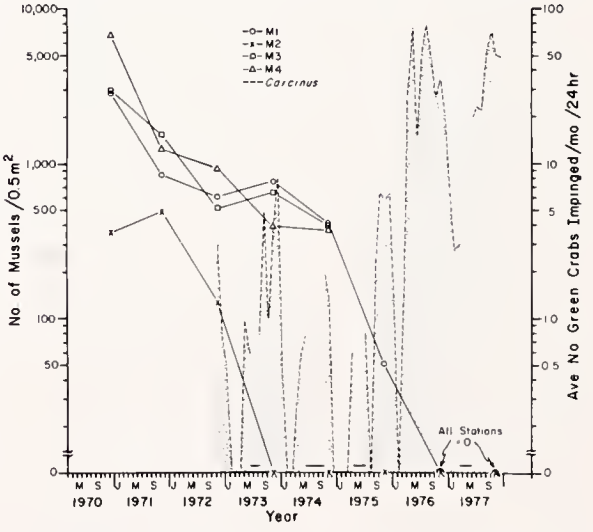

FIGURE 2. *Number of mussels found at four intertidal stations during fall sampling periods, 1970-1977. Also shown is the monthly average number of green crabs caught on the intake traveling screens per 24 hour period at the Maine Yankee Atomic Power plant, November 1972—December 1977. Horizontal lines near the bottom of the figure indicate periods when the plant was shut down.*

discharge plume approximately 15 m from the weir they obtained 98% mortality in 1973 and 100% mortality in 1974. Their next station was about 1.1 km from the weir where mussels experienced 55 and 25% mortalities during 1973 and 1974, respectively. These mortalities may seem high in view of the apparent "normal" situation which was found at the closer intertidal mussel station M3 mentioned above. Mortalities of rafted mussels were probably higher than the intertidal populations because the former remained in the surface water layers while the latter population was alternately exposed to the thermal plume and exposed to the air. Pearce (1969) found that *M. edulis* could withstand substantially high temperatures (30 C) when subjected to a cyclical temperature regime (20, 25, 30, 25, 20, 25 C, etc. for 6 hr each) than when subjected to constant elevated temperatures. Widdows (1976) also found that *M. edulis* which were acclimated to cyclic temperatures between 21 and 29 C had a "higher scope for growth" at 29 C and were less severely stressed than those mussels maintained at a constant temperature of 29 C.

While recruitment of mussel spat on ropes suspended from rafts was several orders of magnitude less in Montsweag Bay than in either the Sheepscot or Damariscotta Rivers during the period 1973-1975 (Lutz and Porter, 1977), recruitment (maxima recorded were 4,100, 300, and 800/m^2 for years 1973-1975, respectively) should have been enough to sustain the intertidal populations on vertical rocky surfaces. The latter populations, however, were declining rapidly (Figure 2), yet mussels continued to be a serious fouling problem on vertical walls of the MY intake structure and within the tubes of the MY cooling condensers through 1977 (Stephen D. Evans, personal communication). Since 2 May 1975 was the last date thermal effluents were discharged into Bailey Cove, recolonization by mussels at M2 was anticipated. No mussels, however, were found during November sampling periods in 1975-1977 (Table 1). In fact, no mussels were found at any stations in 1977 (Table 1).

During October and November, 1977, my associates and I made a diligent search for *M. edulis* on rocky intertidal surfaces throughout Montsweag Bay, including east and west shorelines, islands,

TABLE 1. Mytilus edulis. *Sizes (mm) and numbers of mussels removed from five 0.1m^2 quadrats on vertical rocky surfaces at four stations during fall sampling periods, 1970-1977.*

Sampling period	M1				M2				M3				M4			
	Min	Max	Mean	Total	Min	Max	Mean	Total	Min	Max	Mean	Total	Min	Max	Mean	Total
Dec. '70	2	42	15.5	2,827	2	38	15.0	358	2	38	13.8	2,938	2	62	9.2	6,378
Nov. '71	2	38	17.1	850	6	34	21.0	491	2	38	17.7	1,535	2	62	16.1	1,216
Nov. '72	2	38	18.7	618	6	42	24.4	127	6	58	17.4	515	2	62	22.0	930
Nov. '73	2	42	19.7	764	0	0	0	0	2	42	20.4	649	2	70	26.5	397
Nov. '74	6	38	22.0	411	0	0	0	0	2	30	17.0	400	2	54	22.5	372
Nov. '75	2	42	20.4	51	0	0	0	0	Not Sampled				Not Sampled			
Nov. '76	0	0	0	0	0	0	0	0	Not Sampled				Not Sampled			
Nov. '77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. Carcinus maenas. *Carapace widths of green crabs trapped on traveling screens of the Maine Yankee plant, 1972-77.*

Year	Carapace widths (cm) Min	Max	Mean	Total Crabs	Number of Sampling periods
1972	4	6	4.54	13	8
1973	4	8	6.19	84	47
1974	5	9	6.68	19	36
1975	3	10	6.87	103	44
1976	4	9	6.56	1,535	48
1977	5	10	7.50	1,083	37
					220

and ledges which became exposed at low tide. Almost without exception, the only places where mussels were found were in deep crevices, on the undersides of rocks, or burried in compact sediment between rocks with only about 3-7 mm of their posterior shells visible. As one pulled aside the attached algae (*Ascophyllum nodosum* and *Fucus vesiculosus*) to look for mussels, green crabs (*Carcinus maenas*) of many sizes would scurry for cover. It thus seemed possible that the decline of intertidal mussel populations might be due to an increase in populations of the predaceous green crab. Floats at two docks in the area were examined. Their undersides were festooned with mussels of more than one year class, including young-of- the-year. The nearby intertidal rocky surfaces were as described above. Since the floats were inaccessible to the crabs, it added further circumstantial evidence that crabs were responsible for the decline of mussel populations.

Estimates of temporal changes in *Carcinus maenas* populations were obtained from MY. Stipulations in the Operating License of MY require, in part, that a detailed analysis of one 24 hr sample per week be conducted by species, size and quantity of fish, lobsters and crabs impinged on the intake screens whenever the plant is in operation. The intake screens consist of endless belts of 1 cm mesh wire fencing, one for each of the four circulating pumps. At approximately 2 hr intervals, each screen is rotated to a new position and the impinged objects from the previous time period are dislodged by back flushing, with the dislodged material being returned to the Bay by means of a sluiceway. Ordinarily, back flushing does not occur during the period of about 2 hrs before to 2 hrs after low water to ensure that the dislodged material is returned into tidal waters rather than onto a barren tidal flat. For the weekly 24 hr detailed analyses, all contents dislodged by back flushing are retained by a net (0.5 cm mesh) placed in the sluiceway. A total of 220 24 hr samples were taken between 10 November 1972 and 28 December 1977. Carapace widths of crabs were recorded to the nearest cm. Data thus obtained for impinged *C. maenas* are plotted in Figure 2 as monthly averages. Data on carapace widths are summarized in Table 2. Mussel densities from Table 1 have also been plotted on Figure 2. The abundance of green crabs increased dramatically from the fall of 1972 to 1976 and 1977. This increase coincided with the decline of mussels in 1975, the absence of mussels in 1976 and 1977, and the lack of recolonization by mussels at M2. While there are no quantitative data on green crab abundance during the early part of the study period, it can be inferred that green crab populations were at relatively low levels. Welch (1968) attributed the general decline in green crab abundance in northern New England from the mid-1950's to 1967 to be associated with particularly cold winters and a cooling trend in the water. Figure 3 shows the cooling trend described by Welch and the subsequent warming trend. Although the recent warming trend began in 1968, it must have taken a few years for *Carcinus maenas* population levels to increase substantially. The size of *C. maenas* sampled in the fall of 1972 (Table 2) indicates that the crabs were 3 years old or older (Klein Breteler, 1975). In 1969, a graduate student at the marine laboratory tried to do a thesis research project on *C. maenas*. She

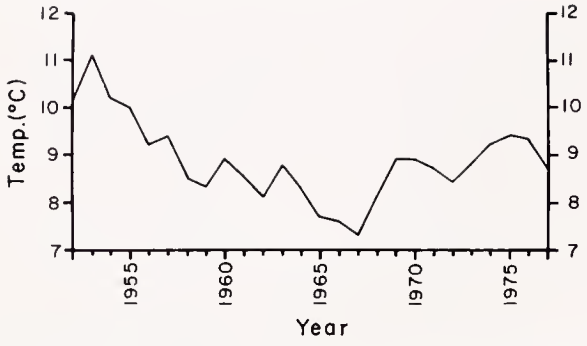

FIGURE 3. *Annual mean surface seawater temperatures at West Boothbay Harbor, Maine, 1954-1977. These data were provided through the courtesy of Mr. Walter R. Welch, Maine Department of Marine Resources, Fisheries Research Station, West Boothbay Harbor, Maine.*

abandoned the project because she could not obtain sufficient numbers of specimens, either by trapping or by hand collecting in the intertidal zone.

Walne and Dean (1972) found that *Carcinus maenas* ate *Mytilus edulis* in all seasons of the year with feeding taking place at temperatures as low as 2.3 C. Maximum feeding rates, however, occurred during the period May-September. They also found that the larger the number of available prey, the greater the predation rate by crabs. Regardless of the size of crabs tested, they tended to eat greater numbers of the smaller sized mussels offered as food. It should be noted that the mean size of mussels tended to increase with time (Table 1) indicating that either recruitment was decreasing or more of the smaller size classes were being eaten by predators or both.

Ropes (1968) examined the stomach contents of 3,979 green crabs and noted that the bivalve molluscs *M. edulis*, *Mya arenaria*, and *Gemma gemma* were the principal food items. *Mytilus* was the most frequent species found in the stomachs. While there are several reports on the impact of green crabs on *Mya* populations (Smith and Chin, 1953; Glude, 1955; Medcoff and Dickie, 1955; Smith et al., 1955; MacPhail et al., 1955; and Welch, 1968), and a record of predation on relaid seed mussels (Dare and Edwards, 1976), no previous publications have been found which document the impact of green crabs on natural mussel populations.

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LITERATURE CITED

Bruce, J. R. 1926. The respiratory exchange of the mussel (*Mytilus edulis* L.). Biochem. J. 20:829-846.

Dare, P. J. and D. B. Edwards. 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Straits, North Wales. J. Cons. Int. Explor. Mer 37:16-28.

Dow, R. L. and D. E. Wallace. 1954. Blue mussels (*Mytilus edulis*) in Maine, Department of Sea and Shore Fish. Bull., Mimeo, Rep., 5 pp.

Glude, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans. Amer. Fish. Soc. 84:13-26.

Hess, C. T., C. W. Smith, and A. H. Price, II. 1975. Model for the accumulation of radionuclides in oysters and sediments. Nature 258:225-226.

Hutchins, L. W. 1947. The bases for temperature zonation in geographical distribution. Ecol. Monogr. 17:325-335.

Klein Breteler, W. C. M. 1975. Growth and moulting of juvenile shore crabs, *Carcinus maenas*, in a natural population. Neth. J. Sea Res. 9:86-99.

Lutz, R. A. and B. Porter. 1977. Experimental culture of blue mussels (*Mytilus edulis* L.) in heated effluent waters of a nuclear power plant. Proc. 8th Ann. Meeting, World Mariculture Soc., Louisiana State University Press, 427-445.

MacPhail, J. S., E. I. Lord, and L. M. Dickie. 1955. The green crab—a new clam enemy. Fish. Res. Board Can., Progr. Rep. Atl. Coast Sta. 63:3-11.

McCleave, J. D. and S. M. Fried. 1974. Three unusual shortnose sturgeons (*Acipenser*

brevirostrum) from Montsweag Bay, Maine. Can. Field Nat. 88:359-360.

McCleave, J. D. and S. M. Fried. 1975. Nighttime catches of fishes in a tidal cove in Montsweag Bay near Wiscasset, Maine. Trans. Amer. Fish. Soc. **104**:30-34.

Medcoff, J. C. and L. M. Dickie. 1955. Watch for the green crab—a new clam enemy. Fish. Res. Board Can., Atl. Biol. Sta. St. Andrews, N. B., Gen. Ser. Circ., 26, 1.

Pearce, J. B. 1969. Thermal addition and the benthos, Cape Cod Canal. Chesapeake Sci. 10:227-233.

Price II, A. H., C. T. Hess, and C. W. Smith. 1976. Observations of *Crassostrea virginica* cultured in the heated effluent and discharged radionuclides of a nuclear power reactor. Proc. Natl. Shellfish. Assoc. 66:54-68.

Recksiek, C. W. and J. D. McCleave. 1973. Distribution of pelagic fishes in the Sheepscot River—Back River Estuary, Wiscasset, Maine. Trans. Amer. Fish. Soc. **102**:541-551.

Ritchie, J. 1927. Reports on the prevention of the growth of mussels in submarine shafts and tunnels at Westbank Electric Station, Portobellow. Trans. R. Scott. Soc. Arts **19**:1-20.

Ropes, J. W. 1969. The feeding habits of the green crab, *Carcinus maenas* (L.). Fish. Bull. 67:183-203.

Scattergood, L. W. and C. C. Taylor. 1949. The mussel resources of the North Atlantic region. Part I. The survey to discover the locations and areas of the North Atlantic mussel-producing beds. Comm. Fish. Rev. **11**:1-10.

Smith, O. R. and E. Chin. 1953. The effects of predation of soft clams, *Mya arenaria*. Conv. Add. Nat. Shellfish. Assoc. 1951, 37-44.

Smith, O. R., J. P. Baptist, and E. Chin. 1955. Experimental farming of the soft-shell clam, *Mya arenaria*, in Massachusetts, 1949-1953. Commer. Fish. Rev. **17**:1-16.

Target, T. E. and J. D. McCleave. 1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Amer. Fish. Soc. **103**:325-330.

Vadas, R. L., M. Keser, and P. C. Rusanowski. 1976. Influence of thermal loading on the ecology of intertidal algae. *IN* Thermal ecology II, G. W. Esch and R. W. MacFarlane, eds. ERDA Symp. Ser. (CONF-750425), Augusta, Ga., 202-212.

Vadas, R. L., M. Keser, P. C. Rusanowski, and B. R. Larson. 1976. The effects of thermal loading on the growth and ecology of a northern population of *Spartina alterniflora*. *IN* Thermal ecology II, G. W. Esch and R. W. MacFarlane, eds. ERDA Symp. Ser. (CONF-750425), Augusta, Ga., 54-63.

Walne, P. R. and G. J. Dean. 1972. Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria*, J. Cons. Int. Explor. Mer **34**:190-199.

Welch, W. R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. Fish. Bull. 67:337-345.

Wells, H. W. and J. E. Gray. 1960. Seasonal occurrence of *Mytilus edulis* on the Carolina coast as a result of transport around Cape Hatteras. Biol. Bull. **119**:550-559.

Widdows, J. 1976. Physiological adaptation of *Mytilus edulis* to cyclic temperatures. J. Comp. Physiol. **105**:115-128

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GENETICS OF SEX DETERMINATION IN THE AMERICAN OYSTER[1,2]

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ABSTRACT

Five families of oysters have been sexed for their first four reproductive years. The sex ratios and frequency of sex changes varies between families. This supports the model of sex determination based on 3 or more gene loci with alternate male and female alleles at each locus.

INTRODUCTION

A model of sex determination in the American oysters (*Crassostrea virginica* Gmelin) has been proposed (Haley 1977). The model suggests that sex is determined by a minimum of 3 genes with additive male and female alleles (Table 1). Assuming each gene has two alternative alleles for sex, (male or female) then each individual has six sex genes with 7 possible genotypes. It was proposed that oysters with three or more male alleles are male, those with 0 or 1 male allele (i.e. 5 or 6 female alleles) are female and combinations of 2 male and 4 female alleles can change sex. This model was proposed from an analysis of sex ratios and sex changes in 5 families of oysters in the first two breeding seasons. The same families were sexed for 2 additional breeding seasons and this paper presents the results for the first 4 breeding seasons.

MATERIALS AND METHODS

In May 1973 six families of oysters were produced at the Fisheries and Marine Services Biological Station at Ellerslie, Prince Edward Island. Three males were each mated to two different females. In 1975 a random sample of 100 to 300 oysters from 5 of these families was made available for this study. A number was glued on each oyster so they could be identified for a number of years. The oysters were naturally conditioned near the station and were sexed by spawning using 30 °C sea water and gonad extract

TABLE 1. *Model of sex determination in oysters with three loci, a, b, c and two alleles each m, f.*

Genotype	No. male alleles	No. female alleles	Proposed sex
$a^m a^m b^m b^m c^m c^m$	6	0	male
$a^m a^f b^m b^m c^m c^m$ etc.	5	1	male
$a^m a^f b^m b^f c^m c^m$ etc.	4	2	male
$a^m a^f b^f b^f c^m c^m$ etc.	3	3	male
$a^m a^f b^f b^f c^m c^f$ etc.	2	4	predominantly males in early years; changing to females
$a^m a^f b^f b^f c^f c^f$ etc.	1	5	female; possibly can change sex
$a^f a^f b^f b^f c^f c^f$	0	6	female

[1] *This research was supported by a grant from the National Research Council of Canada.*
[2] *The author is indebted to the Canada Fisheries and Marine Services Biological Station at Ellerslie, P.E.I. for providing all materials and lab facilities used in conducting this work.*

TABLE 2. *Frequency of males and females in the first four breeding seasons and frequency of sex changes in oysters sexed for 2 or more years.*

Fam-	Parents	Fe-		Sexed in 1975	1976	1977	1978	Oysters sexed for 2, 3 or 4 years: Total numbers	♂ only	changed sex	♀ only	Oysters sexed for 3 or 4 years: Total number	♂ only	changed sex	♀ only
1	1	1	# sexed	43	230	93	88	138	63.0	30.4	6.5	65	60.0	36.9	3.1
			% female	11.6	11.3	28.0	34.1								
2	2	3	# sexed	23	233	107	119	162	44.4	46.3	9.3	72	38.9	51.4	9.7
			% female	4.3	11.1	43.0	52.9								
3	2	4	# sexed	29	208	59	30	89	41.6	33.7	24.7	37	37.8	45.9	16.2
			% female	31.0	33.2	45.8	51.7								
4	3	5	# sexed	8	52	19	30	35	51.4	28.6	20.0	15	33.3	46.7	20.0
			% female	62.5	28.8	47.4	30.0								
5	3	6	# sexed	25	76	32	36	50	42.0	32.0	26.0	31	41.9	32.3	25.8
			% female	48.0	34.2	43.8	50.0								
TOTAL			# sexed	128	799	310	303	474	49.6	36.5	13.9	220	45.0	43.2	11.8
			% female	25	20.3	39.4	49.5								

from other sexually mature oysters as a stimulation.

In the first breeding season (July 1975) 128 out of about 1100 oysters were spawned. In the second season (1976) 96.5 percent of the surviving 850 were spawned. In the third season (1977) about half the remaining 650 were spawned and in the fourth season (1978) approximately 66% of the surviving 460 were spawned.

RESULTS

The combined data from all families shows there is an excess of males in the first two breeding seasons but by the fourth breeding year there is an equal distribution of males and females (Table 2). This pattern has been well known from earlier published results (Galtsoff, 1964). However, there are significant differences between families. Families 2, 3 and 5 have approximately 50:50 sex ratios by the fourth season whereas Family 1 still has an excess of males. (Family 4 has had quite low numbers). The sex ratios change from year to year because a number of oysters change sex. Table 2 shows the frequencies of sex change in oysters sexed for 2 to 4 years. There are family differences in the frequency of sex changes. Family 1 initially had approximately 89% males and about 30% of these males changed sex. Family 2 had about the same initial frequency of males but a greater proportion have changed sex. Families 3, 4 and 5 had a significant number (20-25%) that had remained as females.

The sex changes are predominantly male to female (Table 3). Only 9.2% of the total sex changes were female to male. 71 of the 162 females that had spawned in 1976 were also sexed in 1977 or 1978 and 12.7% had changed to males. 361 of the 637 males that spawned in 1976, were sexed in subsequent years and 39.1% had changed sex. Thus females have a much lower frequency of changing to males. 220 oysters were spawned for 3 or 4 years but only 24 of these have undergone multiple sex changes (Table 3).

DISCUSSION

The sex ratios and frequencies of sex changes vary with families. Family 1 has a predominance of fixed males with a fairly low proportion changing sex. Family 2 had an initial high frequency of males but a much higher proportion have undergone sex changes to females. Families 3, 4 and 5 have a significant fraction (20-25%) of fixed females. These differences can be explained by the proposed model of sex determined by 3 or more gene loci (Figure 1). Family 1 probably consists of a distribution of genotypes towards maleness with a lower number in the combinations that change sex. Family 2 sex genotypes have a large proportion that can change sex but have few fixed females. Families 3, 4 and 5 have sex genotype distributions mainly overlapping fixed female and sex change ranges. (Figure 1 shows lines of about the same length indicating a symmetrical distribution for each family. One would in fact expect

TABLE 3. *Types of sex changes in oysters sexed for 2, 3 or 4 years.*

Family	male to female (♂♀, ♂♂♀, ♂♂♂♀ ♂♀♀, ♂♀♀♀, ♂♂♀♀)	female to male (♀♂, ♀♂♂, ♀♀♂, ♀♂♂♂)	♂♀♂	♀♂♀	♂♂♀♂
1	34	4	3		1
2	62	3	9	1	
3	22	4	4		
4	5	2	3		
5	10	3	1	2	
Totals	133	16	20	3	1
% of all sex changes	76.9	9.2	11.6	1.7	0.6

♂ male
♀ female

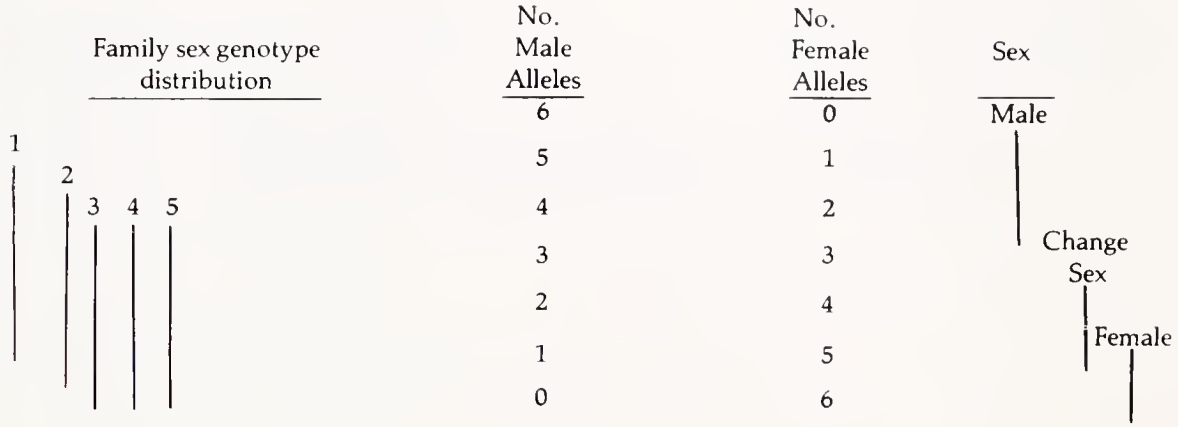

FIGURE 1. *Proposed sex genotype distributions of oyster families.*

quite different distributions depending on the parental genotypes).

The model of sex determination was based on the family differences in sex ratios that indicated some type of Mendelian segregation. The ratios could not be explained by models of one or two loci but could with a minimum of 3 gene loci. The results can also be explained, and indeed the data probably better fit a model with more than 3 loci. The model also suggests sex genotypes with 2 male 4 female alleles and possibly those with 5 female alleles can change sex. It is also possible that some of the 3 male 3 female alleles change sex. Thus, one can propose sex genotypes for the original parents but it does not appear that it could be done with any certainty.

This inability to identify genotypes exactly is normal for traits controlled by many genes. One should however, be able to select lines that are predominantly male or female as Bacci (1965) has done in a hermaphrodite polychaete worm *Ophryotrocha puerilis*).

LITERATURE CITED

Bacci, G. 1965 Sex determination and genic balance of *Ophryotrocha puerlis* a hermaphrodite polychaete worm. Nature 207: 208.

Galtsoff, P.S. 1964 The American Oyster *Crassostrea virginica* Gmelin. Fisheries Bulletin of the Fish and Wildlife Service, U.S. Dept. of the Interior, Vol. 64.

Haley, L.E. 1977 Sex determination in the American oyster. J. of Heredity 68: 114-116.

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EFFECTS OF CULTURAL CONDITIONS ON MORPHOLOGY OF THE SHELL OF THE OYSTER *CRASSOSTREA VIRGINICA*

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ABSTRACT

Morphological and mineralogical characteristics of shells of Crassostrea virginica *were studied in oysters cultured in three well-monitored environments in Lewes, Delaware: a natural area with excellent growth (Broadkill River), a cultural system in which water was changed every second day ("flow-through"), and a cultural system utilizing largely recycled water ("recycle"). Shells from recirculating systems were, in all regards except size, normal in comparison with shells of naturally grown oysters; there were no obvious deformities or anomalies associated with culturing. Cultural system did not affect valve shape, strength, or mineralogy, but did affect valve size and coloration, valve density, prism size, and growth banding patterns.*

Recycle valves, which contained almost no chalky deposits, were thicker and denser than flow-through valves. Field oysters were larger and more pigmented than oysters grown in recirculating systems, and direction of their growth axis was more variable. Surface area of prisms on inner surfaces of the prismatic zone increased with distance from shell margin in all oysters, due to fusion of older prisms. Prisms of faster growing field oysters were significantly larger than prisms of cultured oysters.

Growth bands were absent in the foliated layer, but present on surfaces of chondrophores and nymphae. Subtidal Broadkill oysters deposited approximately 2 growth bands per day, while cultured oysters deposited 4 to 5 bands per day. The pattern of growth bands changed markedly at the chondrophore-nymphal interface, so that approximately 6 times as many bands were present on the nymphal as on the chondrophoral surface.

INTRODUCTION

The study of intensive, controlled bivalve maricultural systems has properly emphasized efforts to improve the rates of growth of both molluscs and algae. Yet there are several other important aspects of the ecology and biology of these systems which need attention. One of these is shell growth and structure and the underlying physiological and biochemical processes of shell formation.

In cultured oysters, shell structure is important in determining the quality of the commercial product. Shells grown under unfavorable conditions are often thin and fragile (Galtsoff, 1964). Medcof (1944) noted that weak, light, and irregular shells are easily damaged during handling and shipping,

and that such damage may affect keeping quality; these unfavorable shell characteristics are attributable, structurally, to a high percentage of chalky material, rather than foliated calcite, in the shell. Ideally, for commercial purposes, an oyster shell should be well-cupped (thick relative to its length), of acceptable form and strength without undue thickness, and lacking excessive amounts of chalky deposits.

Individual environmental factors may exert a marked influence on the morphological characteristics of bivalve shell (Seed, 1968). Clark (1971), for instance, concluded that two subspecies of *Leptopecten latiauratus* in California are, in fact, environmental varieties, and that morphological differences in shell structure are due to differences in temperature between the habitats where the two "subspecies" are found. In the case of *Argopecten gibbus* in Harrington Sound, Bermuda, strong variations in shell convexity with depth were correlated with turbulence (Clark, 1976).

The effect of environment upon shell morphology is particularly pronounced in oysters, in which the principal axes of shell growth are not as permanent as they are in clams, scallops, and other bivalves (Galtsoff, 1964). Lison (1942) pointed out that the shape of an oyster shell cannot be expressed in precise geometrical terms because of its great variability. A list of factors suspected of affecting shell morphology in *Crassostrea virginica* and other ostreids is a long one. Oysters growing singly on firm bottom have a tendency to develop round shells, with poorly developed umbones, ornamented with radial ridges and foliated processes; specimens living on soft muddy bottoms, or those which form clusters and reefs, are, as a rule, long, slender, strongly beaked, and sparsely ornamented (Galtsoff, 1964). Shaw (1965) showed that *C. virginica* grows almost twice as fast when suspended from rafts as on the bottom, and Carreon (1973) found variation in shell shape of *C. iredalei* cultured in the Philippines with various bottom and off- bottom techniques. Thickness of *Crassostrea* valves increases with increasing temperature or current velocity (Ruddy, Feng, and Campbell, 1975) and with increased turbidity levels (Key, Nunny, Davidson, and Leonard, 1976); on the other hand, thickness is reduced by pollution (Frazier, 1976). Salinity changes are suspected of causing blistering (Korringa, 1951) or excessive deposition of chalky shell (Medcof, 1944). Finally, Medcof and Kerswill (1965) attributed a wide variety of morphological variations — in length, cuppedness, symmetry, color, chalkiness, and condition index — to exposure to direct sunlight.

The present study is an attempt to better understand these complex interactions between environmental conditions and shell morphology of the bivalve *Crassostrea virginica* (Gmelin). Sibling oysters were reared in a variety of environments, both natural and closed-system, and a range of characteristics of shell from each environment was studied. This report will concentrate on aspects of shell morphology and mineralogy; future papers will be concerned with shell ultramorphology and chemistry.

MATERIALS AND METHODS

Culture methods for larvae and spat.

All oysters for this study resulted from a single spawning (May 26, 1977) of two brood stock oysters originally collected in the Broadkill River, Delaware. Larvae and spat were raised in the maricultural facility of the College of Marine Studies, University of Delaware, Lewes, Delaware (Pruder, Bolton, Greenhaugh, and Baggaley, 1976), in 400 *l* conical fiberglass tanks. Every other day, seawater in the tanks was changed and larvae were fed a mixture of *Thalassiosira pseudonana* 3H Hasle et Heimdal and *Isochrysis galbana* Parke at an initial concentration of roughly 50,000 cells ml^{-1}. After 17 days, pediveligers were allowed to set onto large rectangular sheets of mylar film until spat density was approximately $1/cm^2$. The mylar was cut into 6 pieces, each inserted into a plexiglass frame, and spat were held in large fiberglass tanks at 27C with a surplus of food for another 17 days.

By this time (July 2, 1977) the five-week-old spat averaged approximately 5 mm in height. Each of the 6 mylar sheets was trimmed to fit into a 20 x 30 cm plexiglass frame, and spat were thinned to approximately 100 on each sheet. Two frames were then positioned in each of three environments (designated "Broadkill," "flow-through," and "recycle"), where they remained until collection on September 17, 1977.

Environments.

The Broadkill River is a tidal stream which drains a large portion of *Spartina alterniflora*-dominated Great Marsh, Lewes, Delaware. Oyster frames were positioned under a floating dock in the Broadkill, at a point approximately ¼ mile before it flows through Roosevelt Inlet into Delaware Bay. The estuary in this area is characterized by swift tidal currents, muddy bottom, and extremely high levels of turbidity, particulate organics and dissolved organics (a large clam-processing plant discharges into the Broadkill approximately ¼ mile upstream from the floating docks). Broadkill oyster frames were elevated approximately 1 m off the bottom and oriented horizontally so that the mylar attachment surface faced down. By positioning the oysters with left (attached) valves uppermost, possible effects of siltation and burial on the oysters were eliminated. These frames were removed from the water only 5 times during the 11-week growth period, to rid them and the oysters of fouling organisms, chiefly the tunicate *Molgula manhattensis*.

"Flow-through" and "recycle" refer to two oyster-growing systems at the maricultural facility in Lewes (Pruder and Bolton, 1977). The two systems are similar in physical configuration, but differ significantly in treatment and turnover time of the water. In both systems, oyster frames were positioned in shallow fiberglass tanks, and, as with the Broadkill oysters, oriented so that the mylar attachment surface faced down. The tanks were approximately 200 x 40 x 15 cm and held roughly 500 ℓ. Oysters in both tanks were fed once or twice a day on a mixture of *Thalassiosira pseudonana* and *Isochrysis galbana* at an initial concentration of 10^5 to 10^6 cells $m\ell^{-1}$. By the next feeding, algal concentration in the oyster tanks was almost always below 10^4 cells $m\ell^{-1}$. In both systems, oysters were removed from the water once daily and rinsed briefly with fresh water. Exposure of oysters to air was normally for less than 1.5 hr, although on 10 of 78 days it extended for 5.5 to 7 hr. Average duration of exposure was 2.0 hr day^{-1}.

All of the water in the flow-through system was changed every two days. Fresh water for this system came from a mixture of Indian River seawater and Lewes city tap water, and was mixed in the oyster tank to an approximate salinity of 20‰. Indian River seawater was passed through one 5 μm and two 1 μm cartridge filters before being pumped into the oyster tank.

In the recycle system approximately 90-95% of the water, also approximately 20‰, was reused daily (Pruder and Bolton, 1977). The only major addition of "new" water to this system was 35 ℓ day^{-1} of *Isochrysis galbana* suspension, cultured in a mixture of Indian River seawater and Lewes tap water. *Thalassiosira pseudonana* was cultured in water from the oyster tanks themselves, after being passed daily through cartridge filters, a protein skimmer, and a charcoal filter. Oysters in both systems were exposed to continuous fluorescent illumination, which was slightly more intense in the recycle than in the flow-through system.

The three oyster growth environments, then, included a natural estuary with excellent oyster growth (Broadkill River), a cultural system utilizing diluted clean seawater changed every two days (flow-through), and a cultural system utilizing largely recycled diluted seawater (recycle). These systems offered a wide range of environments under which oyster growth and shell morphology were monitored.

Environmental monitoring.

Water samples were taken at Canary Creek Bridge, about 200 m south of the oyster frames in the Broadkill, during a concurrent study, and assumed to be representative of water conditions near the oyster docks. Differences in temperature and salinity between the two sites are generally less than 1C and 1‰, respectively (W. Meredith, personal communication). Parameters measured roughly every month during the summer of 1977 included temperature, salinity, dissolved oxygen (DO), particulate organic carbon (POC), particulate organic nitrogen (PON), and dissolved organic carbon (DOC). All measurements were taken hourly over a complete tidal cycle. Salinity was measured with a refractometer, DO by Winkler titration, POC and PON by the method of Sharp (1974), and DOC by the method of Strickland and Parsons (1972).

In each of the cultural systems, data were available daily for the following: temperature, pH, and number of cells of *Isochrysis galbana* and

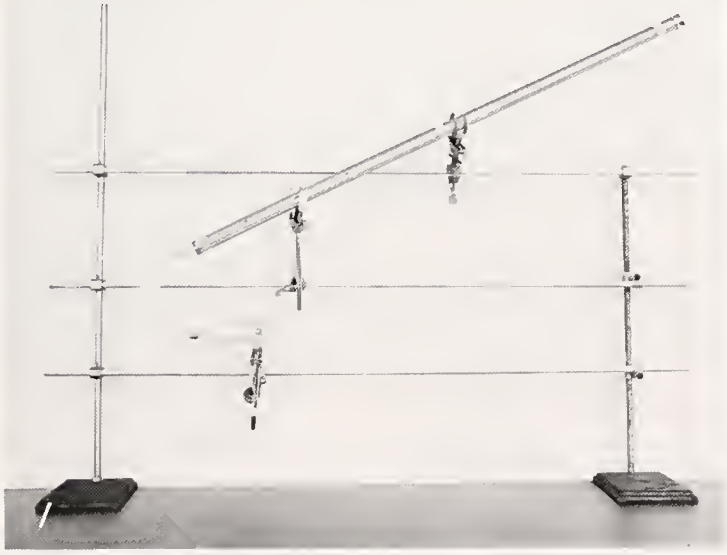
Thalassiosira pseudonana provided as food per gram of oyster. Data recorded on a weekly basis included salinity, whole weight of all oysters in each system, and calcium concentration in the water, as determined by atomic absorption spectrophotometry.

Morphometric measurements.

After approximately 4 months of growth (May 26 to September 17, 1977), oysters from all three systems were gently popped off the mylar film, and individual measurements of height, length, and total wet weight were taken. About ¼ of the free valve of each oyster was cut away with a diamond saw so that shells could be cleaned of meats. Shells were then dipped in 20% clorox solution for 10 sec, in tap water for 10 sec, dried at 65C for 15 min, and stored. Shell surface area was determined by weighing paper cutouts of the shells.

Two volumeters, based on a design given by Huxley (1971), were constructed for volumetric measurements of individual valves (Figures 1, 2). Traditionally, volumetric measurements of large marine invertebrates have been done in graduated cylinders, but in a cylinder large enough to house the animal, accurate determination of volume is impossible. Huxley's apparatus, originally designed for the determination of volume of individual leaves, circumvents this problem by separating the animal holding chamber (a stout glass cylinder) from the measuring arm (thin capillary tube).

In practice, the animal chamber is filled with a 70:30 volumetric mixture of glycerol:ethanol. The syringe is withdrawn, the ground glass stopper inserted and held with light hand pressure, and the syringe fully depressed and held. The fluid is driven part way up the capillary tube, and a reading taken off the meter stick backing this tube. The syringe and stopper are then withdrawn, and the shell placed into the main chamber. With the stopper held tightly and the syringe depressed, a second reading on the meter stick is recorded. The difference between the two readings, in millimeters, can, with use of a predetermined conversion factor, be translated into shell volume in milliliters. For our purposes, volume of the valves themselves was measured, rather than the volume enclosed by the valves. The apparatus, however, is well-suited for either type of measurement.



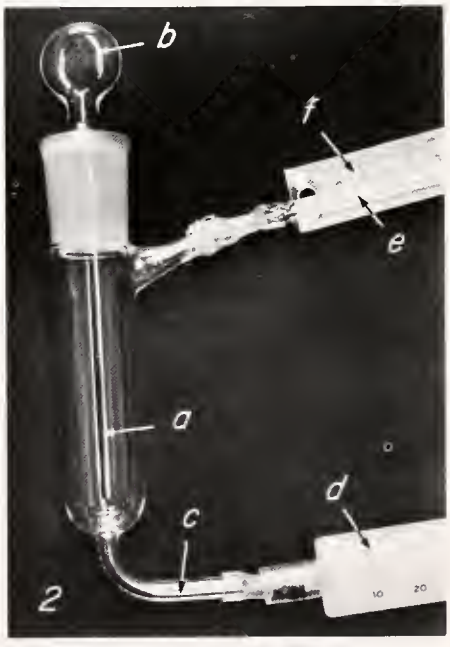


Figure 1. *Overall view, in working orientation, of volumeter used to determine volume of individual oyster shells.*

Figure 2. *Close-up of specimen chamber used to determine volume of individual oyster shells. Components include: (a) specimen chamber (ground-glass joint); (b) ground glass stopper; (c) glass connector; (d) 50cc syringe; (e) capillary tube; (f) meter stick.*

The larger volumeter accepted objects up to 55 mm in diameter, held 20 mℓ, and had a working precision of 0.06 mℓ. For the smaller volumeter, these values were 25 mm, 3.1 mℓ, and 0.01 mℓ. Determination of volume of individual shells allowed accurate calculation of average shell thickness (= volume/surface area) and shell density (= weight/volume).

Prism measurements.

Sizes of individual prisms on the interior of free valves were measured from photomicrographs taken at 400X through a Wild M-20 microscope with epi-illuminator attachment. Five specimens collected on September 17, 1977, from each of the three habitats were chosen for this analysis. On each shell 15 prisms were measured at each of 5 areas: 1) near the growing prismatic edge; 2) 0.25 mm from the edge; 3) 0.50 mm from the edge; 4) halfway from the growing edge to the prismatic-foliated border; and 5) near the prismatic-foliated border. The greatest surface dimension of a given prism was designated "length," and the distance across the surface of the prism midway along the length axis was designated "width." A relative areal measurement was determined by multiplying length by width.

Mineralogy.

Each clorox-cleaned piece of shell (prismatic, foliated, chalky, or ligament) was analyzed by X-ray diffraction by mounting it on the revolving spindle of a Gandolfi camera (Gandolfi, 1967). Shell at the area of adductor muscle attachment (myostracum) and ligament attachment (chondrophore and nymphae) was too thin to isolate in

TABLE 1. *Average values for environmental variables measured in each of three oyster habitats during the period July 2 to September 17, 1977. Ranges shown in parentheses.*

Variable	Broadkill	Flow-through	Recycle
Temperature (C)	23.4	19.2	19.5
	(19.3 - 30.1)	(17.1 - 21.5)	(17.5 - 21.4)
Salinity (0/00)	29.3	20.0	19.0
	(24.0 - 32.0)	(20.0 - 20.5)	(17.0 - 19.5)
pH		7.94	7.88
		(7.69 - 8.27)	(7.71 - 8.08)
DO (ppm)	5.62		
	(2.42 - 9.28)		
kg of oysters in		2.18	2.96
500-ℓ system		(2.00 - 2.36)	(2.77 - 3.15)
T. pseudonana cells		3.78	1.59
per day × 10^{11}		(0.99 - 6.89)	(0.00 - 3.63)
I. galbana cells		3.97	3.97
per day × 10^{10}		(0.00 - 9.80)	(0.00 - 9.80)
Total cells per gram		19.2	6.66
per day × 10^{7}			
POC (mg ℓ^{-1})	3.06		
	(1.44 - 7.22)		
PON (mg ℓ^{-1})	0.37		
	(0.20 - 0.68)		
DOC (mg ℓ^{-1})	3.96		
	(1.74 - 7.13)		
Ca^{++} (ppm)	345[a]	215[b]	163[b]
	(283-377)	(15-343)	(7-300)

[a]Calculated from measured salinities and tables given in Riley and Skirrow (1975).
[b]As determined by atomic absorption spectrophotometry.

pure form for X-ray analysis. In these cases, differentiation of calcite from aragonite was by Feigel's stain (Milliman, 1974).

Shell sections.

Radial sections of shells were prepared after embedding dried shell in Epon 815 resin. Shells were cut along the dorso-ventral axis with a Gillings-Hamco thin-sectioning machine and polished with alumina. Shell was etched with 1% HCl for 10 sec, and acetate peels were prepared of the exposed shell surfaces (Lutz, 1976).

Growth lines.

Attached valves were immersed in 10% clorox for 48 hr. Valves were then separated and residual ligamental material gently removed with a camel's hair brush. The hinge area was cut out with a diamond saw, rinsed well in distilled water, and dried at 60C. Later, shell was mounted onto an aluminum stub with silver paint, freeze-dried for several days, coated under vacuum with carbon and gold, and examined with a Philips PSEM 501 scanning electron microscope.

RESULTS

Environmental conditions.

Table 1 presents mean values and ranges for several environmental variables from the three oyster growth systems. The two cultural systems differed from the natural habitat (Broadkill Rivsr) in having lower, more constant temperatures, lower salinities, and lower calcium concentrations. Mean values for POC, PON, and DOC in the Broadkill highlight the elevated organic content of these waters.

Physical parameters (temperature, salinity, pH) were similar in the two cultural systems. However, approximately three times as many cells were fed to the flow-through oysters on a per gram basis as the recycle oysters. It is interesting that this difference in ration did not produce a significant difference in wet meat production in the two systems (Table 2). Possibly at these temperatures, the assimilative capacity of oysters was saturated at the lower food concentration, so that additional food went unutilized (Kirby-Smith and Barber, 1974).

Differences in calcium concentration in the three systems proved to be marked, indicating the need for careful monitoring of calcium levels in closed cultural systems. Estimated Broadkill values remained well above 250 ppm throughout the summer. Broadkill values were calculated from salinity, a conversion process which assumes that calcium acted as a conservative element in seawater during this period (Riley and Chester,

TABLE 2. *Size parameters of oysters grown in three habitats during the period July 2 to September 17, 1977. All oysters were 114 days old when these measurements were taken. Means from Broadkill oysters taken from sample of n= 8, others from a sample of n = 20. All statistics expressed as means ± 95% confidence interval.*

Measurement	Broadkill	Flow-through	Recycle
Height (mm)	47.40 ± 4.87	21.20 ± 1.56	20.95 ± 1.41
Length (mm)	44.50 ± 4.98	21.30 ± 1.75	19.85 ± 1.38
Height/Length	1.076 ± 0.122	0.999 ± 0.051	1.066 ± 0.066
Wet wt. (g)	9.40 ± 1.553	0.777 ± 0.136	0.978 ± 0.137
Shell wt. (g)	6.06 ± 0.934	0.459 ± 0.093	0.625 ± 0.087
Shell surface area (cm^2)[a]	13.53 ± 2.072	2.994 ± 0.388	2.768 ± 0.199
Shell volume 2 valves (cc)	2.67 ± 0.462	0.200 ± 0.042	0.222 ± 0.030
Shell thickness (cm)	0.197 ± 0.010	0.064 ± 0.007	0.081 ± 0.006
Tissue wet wt. (g)	3.341 ± 0.649	0.352 ± 0.062	0.352 ± 0.054
Shell density ($g\text{-}cm^{-3}$)	2.29 ± 0.130	2.33 ± 0.115	2.81 ± 0.150

[a]Measured for free valve only.

1971). In the two cultural systems, however, calcium levels fluctuated significantly. Low levels were particularly pronounced in the recycle system, where calcium concentration dipped below 150 ppm during 5 of 11 weeks of culture. Rate of calcium deposition is depressed in *Crassostrea gigas* at calcium concentrations in this range (Kado, 1960).

Morphometric measurements.

Oysters grown in the Broadkill during the warm summer period attained a considerably larger size than the cultured oysters (Table 2). Shape, appearance, and solidness (density) of all shells, however, were similar. Height/length ratios of oysters from the three systems were not significantly different ($p>0.05$); all shells were round and well-cupped, although greater variability and shell elongation would be expected if the cultural period were extended beyond 4 months.

"Chalky" areas in oyster shell are dead-white, calcareous areas, which, in limited quantities, are normal constituents of shell. Their fine structure is porous, and in a living oyster the cavities contain sea water; when dried, pieces of chalky shell will actually float (specific gravity of about 0.5). Since pure calcite has a specific gravity of about 2.8, density of dried shell gives an accurate measure of extent of chalky deposits in shell. In general, high densities (above 2.3) indicate solid, strong shells, while low densities (below 2.0) indicate weak, friable, chalky shells.

Shells from all systems were substantial and solid, as indicated by the high density values, but those of the recycle oysters proved to be significantly denser than those from the other two systems (Table 2). Density values indicate that flow-through and Broadkill oyster shells were approximately 25% chalky, while those of the recycle oysters were nearly solidly "pearly," or foliated. Visual observations confirmed these calculations. In all of these juvenile oysters, chalky deposits were confined to the left valve, largely concentrated in a semicircular band along the prismatic-foliated interface, and served to enclose the meats in a flattened, cup-like depression. This specific distribution of chalky deposits was probably related to the flat mylar substratum on which the oysters were set. Visual comparisons indicated that thickness of chalky deposits was much greater in the Broadkill and flow-through oysters than in recycle oysters. Further, although oysters from the two cultural systems did not differ significantly in height or length, recycle shells were significantly thicker than flow-through shells (Table 2). Surprisingly, then, oysters grown in recycled water and exposed to fluctuating and often depressed levels of calcium produced thick, strong shells with a minimum of chalky material.

Morphological observations.

The most noticeable difference in valves from the three habitats was coloration. Broadkill oysters were most vivid, with blotches of yellow, purple, and blue amid a dark brown background. These oysters also showed radiating stripes; in nearly all, a wide yellow band followed the principal axis of growth from umbo to ventrum. Recycle oysters were off-white to pale yellow, and often bore a broad purple-brown band along the principal axis of growth. Flow-through oysters were off-white to pale yellow, but lacked radiating colored bands. Adductor muscle myostracum was brownish in cultured oysters and purplish in Broadkill oysters. None of the oysters were exposed to high-intensity light, either natural or artificial. Broadkill oysters were suspended from the float so that diffuse sunlight could reach them only after penetrating both 0.5 m of very murky water and two layers of translucent plastic. Cultured oysters were exposed to continuous but only moderately bright fluorescent lighting.

The thin, brownish shell layer along the growth margin of the right valve (prismatic zone) was relatively sturdy in Broadkill and recycle oysters, while in flow-through shells, this layer was extremely fragile on both valves. The prismatic zone in oysters may be composed of overlapping scales (Nakahara and Bevelander, 1971), and decorated with fluting (ribs) and other ornamentations. Radial sections of valves from both cultural systems showed many prominent scales, usually over 1 mm in length, while surfaces were covered with flutings and gentle ruffling at the edges. Broadkill oysters were unornamented. No mud blisters from *Polydora websterii* infestation were observed in any of the valves. However, surfaces of Broadkill shells were moderately infested with calcareous tubes of *Hydroides dianthus*.

Although all of these oysters were derived from

TABLE 3. *Size of prisms (μm) ± S.D. on the interior surface of right (free) valves of oysters grown in three habitats. All oysters were sacrificed on September 17, 1977. Each value shown is the mean of 75 measurements (5 oysters per habitat, 15 prisms per oyster), for a total of 375 prisms per habitat. Shell region 1 is at the shell margin, region 2 is 0.25 mm from the margin, region 3 is 0.50 mm from the margin, region 4 is one-half way from the margin to the foliated layer, region 5 is near the foliated-prismatic boundary.* $\bar{X}$ *is the mean of the 5 regions.*

Habitat	Shell Region	Length	Width	Relative Area (μm^2)
Broadkill	1	13.9 ± 5.04	9.0 ± 3.73	140 ± 102.8
	2	15.2 ± 5.31	9.5 ± 3.97	161 ± 119.6
	3	16.1 ± 5.65	10.7 ± 4.31	189 ± 129.1
	4	17.3 ± 5.70	11.6 ± 4.90	223 ± 165.1
	5	22.5 ± 8.32	14.4 ± 5.99	362 ± 269.3
	$\bar{x}$	17.0	11.0	215
Recycle	1	13.6 ± 3.55	8.8 ± 2.71	125 ± 62.0
	2	12.8 ± 4.25	7.9 ± 2.70	108 ± 64.4
	3	15.9 ± 4.52	10.1 ± 3.34	170 ± 87.7
	4	13.9 ± 4.18	9.0 ± 3.14	132 ± 71.0
	5	16.8 ± 6.81	10.2 ± 3.83	187 ± 120.0
	$\bar{x}$	14.6	9.2	144
Flow-through	1	9.5 ± 2.94	6.5 ± 2.23	66 ± 38.8
	2	10.0 ± 3.71	6.3 ± 2.48	70 ± 46.5
	3	11.8 ± 4.18	8.6 ± 6.41	109 ± 82.6
	4	13.6 ± 4.83	9.1 ± 3.47	136 ± 92.1
	5	14.0 ± 4.96	9.5 ± 3.81	149 ± 101.1
	$\bar{x}$	11.8	8.0	106

a single spawning and were attached to a similar substratum, the direction of growth differed greatly in the three systems. When the right valve was viewed from above, over 95% of the shells of cultured oysters curved to the right; in Broadkill oysters, one-half curved to the left, one-half to the right.

Prism measurements.

During the course of this study, the question arose whether mineral prisms deposited at the growing edge of a shell could serve as an indicator of environmental conditions. For instance, would a fast-growing oyster lay down significantly larger prisms than a slow-growing oyster, and could this difference be used as a sensitive indicator of short-term environmental fluctuations? To test this hypothesis, we selected 5 oysters from each habitat, and for each oyster, 15 prisms at each of 5 shell areas on a transect from the shell edge to the foliated shell layer were measured and statistically compared (Tables 3, 4).

Incomplete understanding of the mechanism of shell deposition in oysters makes analysis of these data difficult. There can be no doubt that prisms observed at the interior margin of the shell are recently deposited prisms. However, if an oyster is growing at the rate of 0.1 mm day^{-1}, surfaces of prisms observed 0.5 mm from the growing edge were not deposited 5 days ago. More than likely, they were initiated 5 days ago, but have been added to and thickened by 5 days of periodic mantle activity. What is observed may be an imperfect replica of what was deposited 5 days previously.

In oysters from all three systems, surfaces of prisms interior to the shell edge were significantly ($p<0.01$) larger in length, width, and relative area than surfaces of prisms at the shell edge (Table 3); Table 4 presents statistical confirmation of these trends. In the top half of Table 4, multiple t-tests (Duncan Multiple Range Test) have been applied to determine which shell regions were statistically equivalent in terms of size of prisms contained within them. Such shell regions ars joined by an

TABLE 4. *Statistical comparison of relative area of prisms (μm^2) on the interior surfaces of right valves of oysters grown in three habitats. Duncan Multiple range test, with non-significant (p .05) differences in prism size underlined. Designation of shell regions same as in table 3.*

Habitat	Shell Regions
Broadkill	1 2 3 4 5
Recycle	1 2 3 4 5
Flow-through	1 2 3 4 5

Shell region	Habitat
1	B R F
2	B R F
3	B R F
4	B R F
5	B R F
$\bar{x}$	B R F

underscore. The similarity patterns obtained indicate that many adjacent and nearly adjacent shell regions contained similarly sized prisms, but that there was a significant and steady increase in prism size inward from the shell margin toward the foliated-prismatic interface. This pattern indicates that, as the prismatic layer thickens, fusion occurs between some adjacent prisms. Initiation of fusion is evident where a conchiolin spur extends part way across the surface of a large prism. The incomplete matrix in this case is a remnant of an organic envelope which separated two adjacent prisms prior to their fusion.

Multiple range analyses also indicate that, in general, prisms are larger in faster-growing Broadkill oysters (bottom half of Table 4); relative surface area of an average Broadkill prism was about twice that of an average prism from a cultured oyster (Table 3). Prisms for recycle oysters were, in 3 of 5 shell regions, significantly larger than prisms from flow-through oysters, even though the height and length measurements of oysters from these two systems were virtually identical (Table 2). The larger size of recycle prisms may be partly related to the thicker, sturdier shell produced by recycle oysters. The lack of underscoring on the last line ($\bar{x}$) of Table 4 indicates that the average Broadkill oyster prism is significantly larger than the average recycle oyster prism, which is significantly larger than the average flow-through oyster prism.

A less complete study was also made of the exterior surfaces of free valves from the three habitats. Largest prisms were again formed in the Broadkill oysters. Prism size in a given habitat did not appear to increase with distance from the exterior shell margin. This is not surprising, since the exterior of the valve is isolated from the activity of the mantle, and therefore not subject to prism fusion as is the interior surface. Prism size at time of deposition, then, can only be inferred from looking at the outside of the shell, but only if no severe shell weathering has occurred.

Mineralogy.

A study of the mineral composition of several parts of the oyster shell was undertaken for two reasons: first, to confirm, and in some cases, extend earlier reports of bivalve shell mineralogy (Stenzel, 1963), and second, to ascertain the effect, if any, of cultural conditions on shell mineralogy.

TABLE 5. *Mineralogy of various regions of the shell of* Crassostrea virginica.

Calcite	Aragonite
Foliated layer (Calcitostracum)	Adductor myostracum (point of attachment of adductor muscle)
Prismatic layer	Point of attachment of Quenstadt's muscle
Chalky deposits[a]	Calcified portions of ligament
Chondrophore[b] of attached (left) valve	Chondrophore[b] of free (right) valve
Nympha[c] of attached (left) valve	Nympha[c] of free (right) valve

[a]Traces of aragonite may be found in chalky deposits

[b]Point of attachment of resilial portion of ligament

[c]Point of attachment of tensilial portion of ligament

The results are summarized in Table 5. Shell mineralogy was identical in oysters from the three cultural systems.

Waller (1976) found that the resilium of post-larval *Argopecten irradians* is supported by aragonitic shelves formed as continuations of the aragonitic prodissoconch. To our knowledge, with this exception, data presented here on mineralogy of chondrophores and nymphae are the first reported in the molluscan literature. Data from all other regions of the shell are in agreement with previously published results for the Ostreidae (Taylor, Kennedy, and Hall, 1969).

Growth lines.

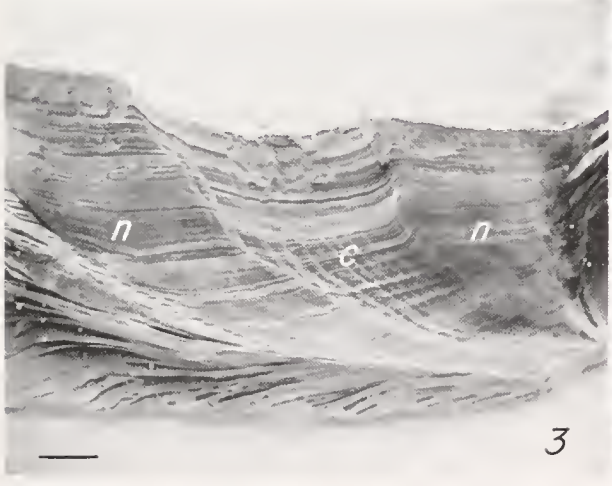
We had hoped to identify periodic, possibly daily, growth lines in radial sections of oyster shell. If such lines were present it would be theoretically possible to identify the effect of various environmental conditions on short-term growth. Unfortunately, as Lutz (1976) found in his search for annual growth lines in *Crassostrea virginica*, daily or circadian growth bands are not present in the foliated layer of the oyster.

Scanning electron micrographs of sections of the ligament did reveal fine striations, but the organic nature of this structure and the difficulty of preparing polished sections from it made the ligament unsuitable as an ultrastructural indicator of possible growth bands. However, surfaces of the hinge to which the ligament is attached (chondrophores and nymphae) are covered with a thin shell layer in which annulations are clearly evident (Figure 3).

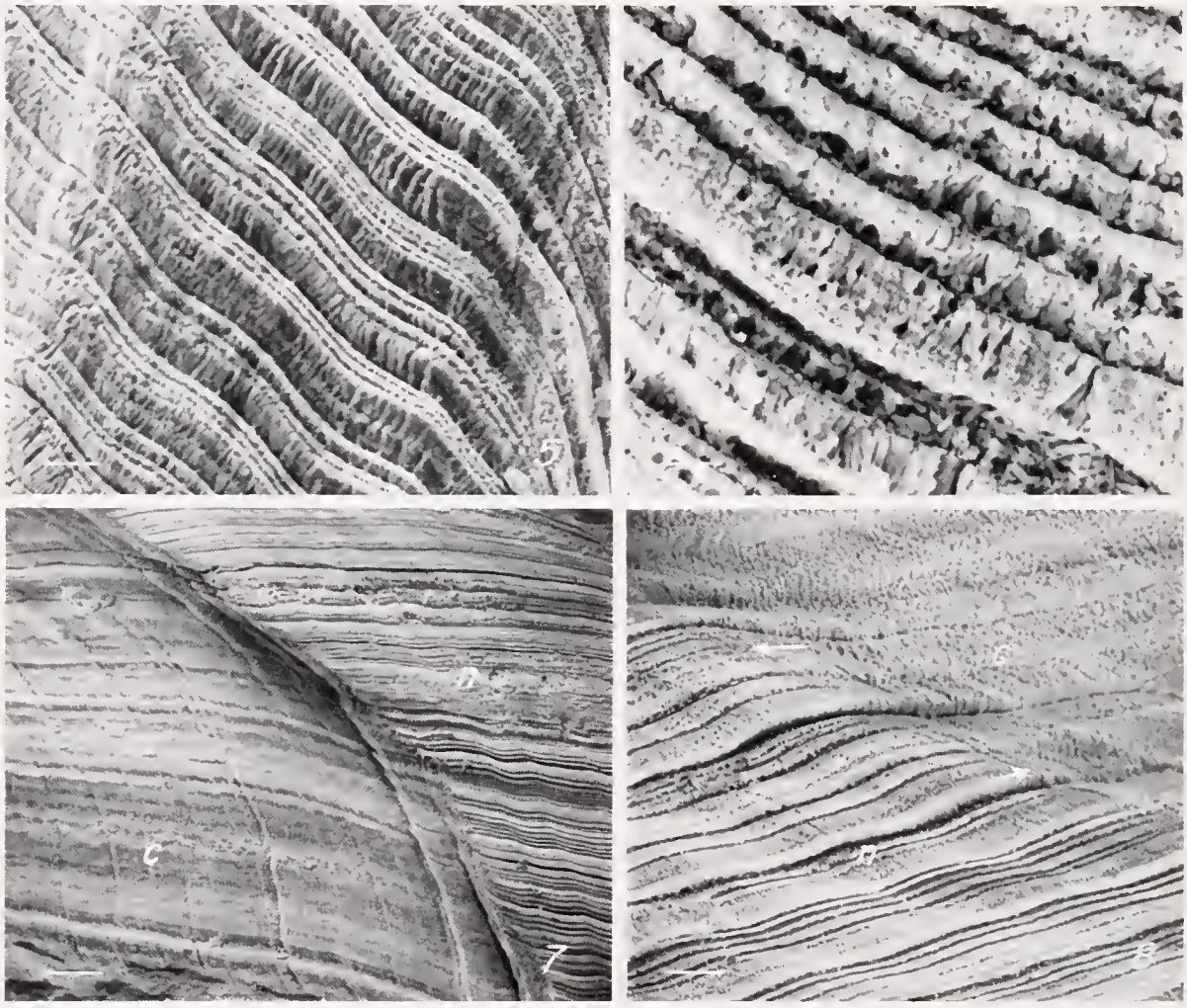
Annulations are much more pronounced on the left valve than on the right valve, and tend to be most distinct on the anterior nympha of the left valve. Annulations are not readily visible on acetate peels of the hinge area, because the shell layer bearing these rings is extremely thin, usually less than 5 μm. These rings are therefore most conveniently studied with the scanning electron microscope, by direct viewing of the surfaces to which the ligament is attached.

On nymphae from Broadkill Creek oysters, rings were relatively evenly spaced (Figure 4). Approximately one ring was present for each tidal cycle. In two Broadkill oysters with a post-larval life span of 96 days, nymphal annulations numbered 200 and 215.

On nymphae from oysters cultured in both recycle and flow-through systems, rings were usually present in a characteristic pattern in which groups of 1 or 2 broad bands were separated by 2 to 6 extremely fine bands (Figure 5). Both thick and thin bands are made visible by removal of



Figures 3-8. *Scanning electron micrographs of surfaces of chondrophores and nymphae of left values of* C. virginica. *All surfaces but that in Figure 4 were etched with 10% clorox for 48 hr to remove the ligament; 4 was etched with 20% clorox for 48 hr. 3. Panoramic view of chondrophore (c) and nymphae (n). Umbo points posteriorly. Scale bar = 450 μm. 4. Nympha of Broadkill Creek oyster, showing relatively evenly spaced growth bands. Scale bar = 30 μm.*



5. Nymphae of cultured oyster (recycle), showing characteristic pattern of thick and thin bands. Scale bar = 20 μm. 6. Nympha of cultured oyster (recycle). Lines separating growth bands are organic-rich areas which were eroded by cloroxing. Scale bar = 6 μm. 7. Transition zone between nympha (n) and chondrophore (c) of cultured (recycle) oyster. Approximately 6 times as many bands on nympha as on chondrophore. Scale bar = 125 μm, 8, Close-up of transitional zone (arrows) between chondrophore (c) and nympha (n) of cultured oyster (recycle). Only major nymphal lines are visible on the chondrophore. Scale bar = 30 μm.

organic-rich areas between adjacent bands with clorox (Figure 6). In cultured oysters an average of 4 to 5 nymphal annulations were formed per day. One flow-through oyster with a post-larval life span of 96 days had 435 nymphal bands; two recycle oysters with the same life span had 411 and 430 nymphal bands.

Curiously, many more bands were present on the nymphae than on the corresponding adjacent chondrophore (Figure 7). The recycle oyster which had 411 nymphal bands showed only 64 annulations on the chondrophoral surface. For one of the flow-through oysters, the nymphal and chondrophoral bands numbered 435 and 75, respectively. Ultrastructurally, the basis for reduction of bands at the chondrophore-nymphal interface is readily apparent (Figure 8). Broad organic-rich layers on the surface of the nympha continue onto the chondrophore, but fine organic-rich layers do not.

DISCUSSION

All of our observations pertain to oysters which were 4 months old or less. Thus, some characteristics of shell reported here may not be present in older oysters, in which other factors may become important. For instance, the narrow distribution of chalky deposits reported here changes to a more random one after a year or two of growth (Galtsoff, 1964). Also, shape of young oysters tends to be round in most environments, with elongation normally expressed later in ontogeny.

Nevertheless, from the viewpoint of closed-system culturists, it is encouraging that shells from recirculating systems were, in all regards except size, normal in comparison with shells of naturally grown oysters. Cultural system used did have an effect on valve size, coloration, and density, but not on valve shape, strength, or mineralogy; more importantly, there were no shell anomalies or deformities associated with intensive closed-system culturing, as Epifanio (1976) found with the bay scallop, *Argopecten irradians*. Frazier (1976) reported that *Crassostrea virginica* produced thin shells in environments with elevated concentrations of heavy metals, and levels of certain metals were higher in both the water and in oyster shells from the recycle system than from the flow- through system (L. V. Sick, personal communication). Nevertheless, recycle oyster shells were thicker and sturdier than the flow-through shells. Thus, from the standpoint of production of commercially desirable shell, the oyster seems amenable to intense culturing and handling in recirculating closed systems.

The rationale for investigating growth lines and prism sizes was that minute ultrastructural or elemental changes might be permanently recorded in shell in response to subtle physical and chemical variations in the oysters' environment. Such responses would be far more sensitive in evaluating growing conditions, particularly in closed cultural systems, than would periodic measurements of shell growth, weight, or condition index. Results of this study suggest that measurement of prisms at the growing edge of the shell, though laborious, might be a useful microindicator of growing conditions; prisms, for example, are larger in faster-growing oysters.

Annulations on chondrophores and nymphae of *Crassostrea virginica* are probably analogous to growth bands reported from the nacreous layer of many other bivalves (Pannella, 1975). Growth lines have not previously been recorded in oysters, apparently because they are not preserved in foliated shell structure. Bands discovered in this study may enable the study of growth increments to be extended to a number of bivalve species in which foliated shell dominates, including many of the Pectinacea, Anomiacea, and Ostreacea.

Interpretation of growth lines in molluscan shell is an evolving science. In many species it appears that lines are faithfully reproduced with every tidal sequence (Berry and Barker, 1975; Evans, 1975), while in other species lines may be produced in response to other exogenous or endogenous factors (Evans, 1975; Pannella, 1975). In some species the number of lines produced per unit time may depend on age of specimen, latitude, and depth of water (Hall, 1975).

The present study was not principally behavioral, so it is impossible to say with certainty what the pattern and density of annulations on the chondrophores and nymphae of *Crassostrea virginica* signify. It is certain, though, that about twice as many bands were produced in cultured as in Broadkill oysters. If growth bands are a response to shell closure and anaerobiosis (Lutz and Rhoads, 1977; Gordon and Carriker, 1978), then multiplication of lines in cultured oysters may be the inevitable result of increased vibration and handling associated with intensive culturing. The number of lines formed on the hinges of Broadkill oysters suggests that, under natural conditions, one line may be laid down with each tidal cycle, but further studies are needed to confirm this.

Preparation of nymphae and chondrophores by methods described here is straightforward, and annulations revealed by these methods might prove useful to culturists in a number of ways. For instance, by exposing an oyster to air for a day to two, one would expect to see a pronounced disturbance line formed on the chondrophores and nymphae (Clark, 1975). Size and number of annulations formed beyond the disturbance line could provide basic information on rhythmicity of shell deposition or feeding processes. These annulations could also serve as microindicators of

very small growth increments; the only methods currently in use for measurements of minute growth increments in bivalves involve considerable disturbance to the living animal (Strömgren, 1975).

The nearly complete absence of chalky calcite from recycle shells and the normal occurrence of this skeletal material in Broadkill and flow-through shells were unexpected. The obvious variable between the two cultural systems which might account for this consistent difference in shell morphology was calcium concentration. Calcium levels were, on the average, lower and more highly fluctuating in the recycle system. This suggests a means for culturists to recoup shell quality in their product should shells become weak and flaky.

The ultimate goals of our studies are diagnosis and prediction. It would be important for culturists to know whether any shell characteristic might provide a sensitive microindicator of oyster health and of normalcy of environmental conditions. Results from this study suggest several morphological and morphometric characters which could be used in this way, including size of prism surfaces at the growing edge, size and pattern of growth increments on the hinge surfaces, and density of individual valves or parts of valves.

This study has qualified what oyster biologists have long known — that environmental conditions can have a great influence on shell morphology. With the exception of the work of Medcof and Kerswill (1965), though, there have been no controlled studies on the effects of single environmental variables on bivalve shell form and growth. The study described here was designed as a searching mission, an attempt to detail growth characteristics of shell in well-monitored environments and to discover microstructural indicators of oyster health and growing conditions. The results suggest that further single-variable controlled studies like Medcof and Kerswill's would be extremely valuable both in understanding and in attempting to modify bivalve shell form. Variables which seem to be most important in this regard (assuming all nutritional problems have been solved) include nature of the substratum, lighting regimes, and calcium levels. In the future, as these environmental interactions are better understood, culturists can begin to consider modification of shell form, appearance, and strength in commercially desirable directions.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Berry, W. B. N. and R. M. Barker. 1975. Growth increments in fossil and modern bivalves. *In* Growth rhythms and the history of the earth's rotation. G. D. Rosenberg and S. K. Runcorn, Eds. John Wiley and Sons, New York, 9-24.

Carreon, J. A. 1973. Ecomorphism and soft animal growth of *Crassostrea iredalei* (Faustino). Proc. Nat. Shellfish. Assoc. 63: 12-19.

Clark, G. R. 1971. The influence of water temperature on the morphology of *Leptopecten latiauratus* (Conrad, 1837). Veliger 13: 269-272.

Clark, G. R. 1975. Periodic growth and biological rhythms in experimentally grown bivalves. *In* Growth rhythms and the history of the earth's rotation. G. D. Rosenberg and S. K. Runcorn, Eds. John Wiley and Sons, New York, 103-116.

Clark, G. R. 1976. Shell convexity in *Argopecten gibbus:* variation with depth in Harrington Sound, Bermuda. Bull. Mar. Sci. 26: 605-610.

Epifanio, C. E. 1976. Shell deformity among scallops *(Argopecten irradians* Lamark)

cultured in a recirculating seawater system. Aquaculture 9: 81-85.

Evans, J. W. 1975. Growth and micromorphology of two bivalves exhibiting non-daily growth lines. *In* Growth rhythms and the history of the earth's rotation. G. D. Rosenberg and S. K. Runcorn, Eds. John Wiley and Sons, New York, 119-133.

Frazier, J. M. 1976. The dynamics of metals in the American oyster, *Crassostrea virginica*. II. Environmental effects. Chesapeake Sci. 17: 188-197.

Galtsoff, P. S. 1964. The American oyster, *Crassostrea virginica* Gmelin. U. S. Fish. Wildl. Serv. Fish. Bull. 64: 1-480.

Gandolfi, G. 1967. Discussion upon methods to obtain x-ray (powder patterns) from a single crystal. Mineral. Petrogr. Acta 13: 67-74.

Gordon, J. and M. R. Carriker. 1978. Growth lines in molluscs: subdaily patterns and dissolution of the shell. Science 202: 519-521.

Hall, C. A. 1975. Latitudinal variation in shell growth patterns of bivalve molluscs: implications and problems. *In* Growth rhythms and the history of the earth's rotation. G. D. Rosenberg and S. K. Runcorn, Eds. John Wiley and Sons, New York, 163-174.

Huxley, P. A. 1971. Leaf volume: a simple method for measurement and some notes on its use in studies of leaf growth. J. App. Ecol. 8: 147-153.

Kado, Y. 1960. Studies on shell formation in Mollusca. J. Sci. Hiroshima Univ., Ser. B1, 19: 163-210.

Key, D., R. S. Nunny, P. E. Davidson and M. A. Leonard. 1976. Abnormal shell growth in the Pacific oyster *(Crassostrea gigas)*: some preliminary results from experiments undertaken in 1975. ICES CM 1976/K:11, Shellfish and Benthos Committee Report, 12 p.

Kirby-Smith, W. W. and R. T. Barber. 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. Aquaculture 3: 135-146.

Korringa, P. 1951. On the nature and function of "chalky" deposits in the shell of *Ostrea edulis* Linnaeus. Proc. Calif. Acad. Sci. 28: 133-158.

Lison, L. 1942. Caracteristiques geometriques naturelles des coquilles de Lamellibranches. Bull. Classe Sci., Acad. Roy. Belg. 5, 28: 377-390.

Lutz, R. 1976. Annual growth patterns in the inner shell layer of *Mytilus edulis* L. J. Mar. Biol. Assoc. U. K. 56: 723-731.

Lutz, R. A. and D. C. Rhoads. 1977. Anaerobiosis and a theory of growth line formation. Science 198: 1222-1227.

Medcof, J. C. 1944. Structure, deposition, and quality of oyster shell *(Ostrea virginica* Gmelin). J. Fish. Res. Bd. Canada 6: 209-216.

Medcof, J. C. and C. J. Kerswill. 1965. Effects of light on growth of oysters, mussels, and quahaugs. J. Fish. Res. Bd. Canada 22: 281-288.

Millimann, J. D. 1974. Recent sedimentary carbonates. Marine Carbonates, Part 1. Springer-Verlag, Berlin, 375 p.

Nakahara, H. and G. Bevelander. 1971. The formation and growth of the prismatic layer of *Pinctada radiata*. Calc. Tiss. Res. 7: 31-45.

Pannella, G. 1975. Palaeontological clocks and the history of the earth's rotation. *In* Growth rhythms and the history of the earth's rotation. G. D. Rosenberg and S. K. Runcorn, Eds. John Wiley and Sons, New York, 253-284.

Pruder, G. D., E. T. Bolton, E. E. Greenhaugh and R. E. Baggaley. 1976. Oyster growth and nutrient nitrogen cost in bivalve molluscan mariculture. Univ. Del., Sea Grant Publ. DEL-SG-11-76, 20 p.

Pruder, G. D. and E. T. Bolton. 1977. System configuration and performance: bivalve molluscan mariculture. Univ. Del., Sea Grant Publ. DEL-SG-1-77, 21 p.

Rilsy, J. P. and R. Chester. 1971. Introduction to marine chemistry. Academic Press, London, 465 p.

Riley, J. P. and G. Skirrow. 1975. Chemical oceanography, Vol. 4, 2nd ed. Academic Press, London, 363 p.

Ruddy, G. M., S. Y. Feng and G. S. Campbell. 1975. The effect of prolonged exposure to elevated temperatures on the biochemical constituents, gonadal development and shell deposition of the American oyster, *Crassostrea virginica*. Comp. Biochem. Physiol. 51B: 157-164.

Seed, R. 1968. Factors influencing shell shape in the mussel *Mytilus edulis*. J. Mar. Biol. Assoc. U. K. 48: 561-584.

Sharp, J. H. 1974. Improved analysis for "particulate" organic carbon and nitrogen from seawater. Limnol. Oceanogr. 19: 980-984.

Shaw, W. N. 1965. Pond culture of oysters — past, present, and future. Trans. 30th North Amer. Wildl. Nat. Res. Conf., Washington, D.C., 114-120.

Stenzel, H. B. 1963. Aragonite and calcite as constituents of adult oyster shells. Science 142: 232-233.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada Bull. 167: 1-310.

Strömgren, T. 1975. Linear measurements of growth of shells using laser diffraction. Limnol. Oceanogr. 20: 845-848.

Taylor, J. D., W. J. Kennedy and A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea — Trigonacea. Bull. Brit. Mus. Supp. 3: 1-125.

Waller, T. R. 1976. The development of the larval and early post-larval shell of the bay scallop, *Argopecten irradians*. Bull. Amer. Malacological Union for 1976: 46 (abstract).

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LARVAL DEVELOPMENT OF THE GEODUCK CLAM (*PANOPE GENEROSA*, GOULD)[1]

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ABSTRACT

Geoduck clams (Panope generosa, *Gould) were conditioned at 9-10 C and spawned in the laboratory using thermal stimulation, sperm suspensions, and algae as spawning inducements. Fertilized eggs were reared to the post-larval stage in 14 C water. Larval development required 47 days, and at metamorphosis the larvae averaged 381 „m in shell length. Photomicrographs and shell measurements of the developing larval stages are included.*

INTRODUCTION

The geoduck (*Panope generosa*, Gould) is an important sport and commercial clam in Washington State. Landings from the Puget Sound, Washington commercial fishery in 1977 were 3.9-million kilograms (8.5-million lb). A commercial fishery has recently developed in British Columbia.

Geoducks can grow to an acceptable commercial size of 0.7 kilograms in about six years (Goodwin, 1976). Post-harvest surveys have shown that geoduck recruitment into commercially harvested beds occurs nearly every year, but at very low rates. The average number of geoducks, four years or younger, counted in 36 transects from three locations was 0.01/m² compared to an average of 0.9/m² of older clams.[2] With the low recruitment rate, it is desirable to reduce the time interval between successive harvests by planting harvested beds with cultured juvenile clams. Planting of intertidal public beaches for sport digging is also a possibility. Geoducks are large and have a high value which could off-set the high costs of the cultured seed.

During the past several years, geoducks have been spawned and their larvae reared through metamorphosis at the Point Whitney Laboratory. In this paper we describe the general conditioning, spawning, and culture techniques found to be most successful. Larval descriptions, photomicrographs, and measurements are included to aid in the identification of geoduck larval stages in plankton samples.

METHODS

General spawning and culture techniques used were developed by Loosanoff and Davis (1963). Photomicrographs and measurements were made following the procedures of Loosanoff et al. (1966).

Spawning

In Puget Sound geoducks spawn in the spring (Goodwin, 1976; Andersen, 1971). Parent stocks

1 The work reported here was partially financed by the National Marine Fisheries Service, Fisheries Research and Development Act, PL 88-309.

2 Goodwin, Lynn. 1978. Project progress report 309. Hardshell clam and geoduck studies. Unpub. Manuscr. State of Wash. Dept. of Fish, Olympia, WA

for our studies were obtained with diver-operated water jets (standard commercial gear) from subtidal beds in southern Puget Sound during October-April when water temperatures are about 8-9 C. The clams were brought into the laboratory and placed in trays with flowing heated seawater from Dabob Bay (salinity 28.8 o/oo ± 0.8SD, n = 36). Water temperature in the trays was maintained at 9-10 C. Clams were held at this temperature for a minimum of two weeks before any attempt was made to induce spawning. During this period no food was added to the unfiltered bay water.

Spawning was induced by raising the temperature from 9-10 C to 14-15 C over a 3-4 hour period. The algae *Monochrysis lutheri* or sperm from a sacrificed male geoduck or both were added as spawning stimulants. Spawning normally began with release of sperm by one or two males from the 20-30 clams in each tray, followed by release of gametes by both sexes. Gametes are released continuously from the excurrent siphon for several minutes to over an hour with occasional violent contractions of the siphons which produce large quantities of sperm or eggs. Spawning females were transferred to small individual containers of unfiltered 14 C seawater to avoid contamination of the eggs and excessive concentration of sperm. Females can produce at least 15-20-million eggs during one spawning but normally less than half this amount are released. The clams can be returned to cooler water and induced to spawn again during the ensuing 1-2 months.

The fertilized eggs, 80 m m in diameter (Figure 1) were cleaned and placed in 650-liter rectangular tanks filled with filtered 14 C bay water at a density of 4,000-10,000 per liter.

Culture Maintenance

The tanks were cleaned and refilled with filtered 14 C seawater two or three times a week. The larvae were held on the appropriate size screens during cleaning. The larvae were then placed in the clean tanks and fed *Monochrysis lutheri, Isochrysis galbana, Pseudoisochrysis paradoxa,* and *Phaeodactylum tricornutum* either singly or mixed at a density of about 50,000 cells/ml.

Mortalities were extremely high (80%-100%) during the early larval stages in the first experiments. In later experiments this mortality has been reduced to 30%-50% with the use of tetracycline hydrochloride at 12 ppm. However, antibiotics did not control the high mortality during metamorphosis (50%--80%) or the constant mortality which occurred after metamorphosis during the first month of post-larval life.

During the spring of 1979, mortality in the early larval stages and during metamorphosis was reduced to less than 5% in cultures raised with and without tetracycline. The sharp decline in mortality from previous experiments is attributed to use of algae cultures which were nearly free of bacteria and to reduction in larval densities throughout the experiments. Straight hinged larvae were raised at a density of 3,000 larvae per liter compared to previous densities of 4,000-10,000 per liter. Density of larvae at the time of metamorphosis was reduced from 400-1,000 larvae per liter in past experiments to

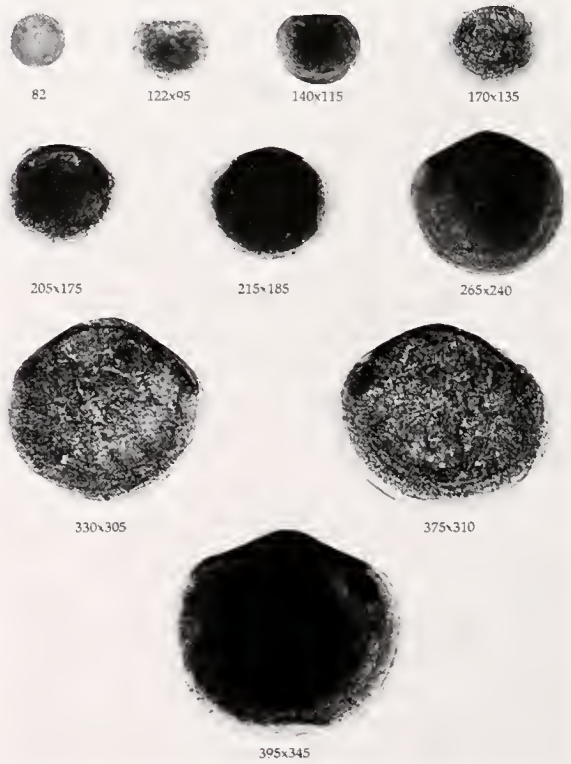
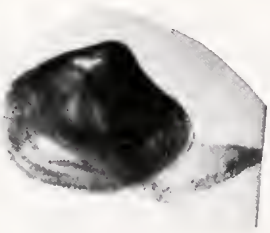
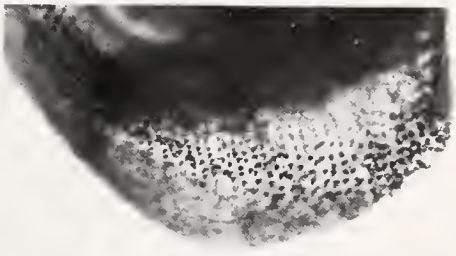


FIGURE 1. *Photomicrographs of a geoduck fertilized egg and larvae from early straight hinge to metamorphosis stage. Length and width measurements given in micrometers.*



Post larvae 800×650

Hinged valves from goeduck
Post-larvae showing line between
Prodissoconch II and dissoconch 500×425



Posterior end of dissoconch shell with spines
725×570

FIGURE 2. *Photomicrographs of geoduck post-larvae, length and width measurements are given in micrometers.*

250 larvae per liter. Tetracycline was not necessary and significantly slowed growth in the post-larvae.

Development of Larvae

Within 2 hours of fertilization the embryos begin to divide and by 48 hours are at the straight hinge stage (Goodwin, 1973). At this stage the prodissoconch 1 is 111 μm ± 5SD (n = 31) in length and 86 μm ± 5SD (n = 31) in width (Figures 1 and 3).[3] Umbones begin to appear at about 165 μm shell length and the larval foot becomes visible at about 300 μm. At 14 C the larvae grow to a length of 381 μm ± 19SD (n = 62), [the average maximum length of the prodissoconch 11 measured in post-larval clams (Figures 2 and 4),] in about 47 days. Larvae held at 17.6°C without tetracycline grew to a length of 377 μm ±46 SD (n=14) in 30 days. In some cultures larvae lose

3 Length = maximum anterior-posterior dimension
Width = maximum dorsal-ventral dimension

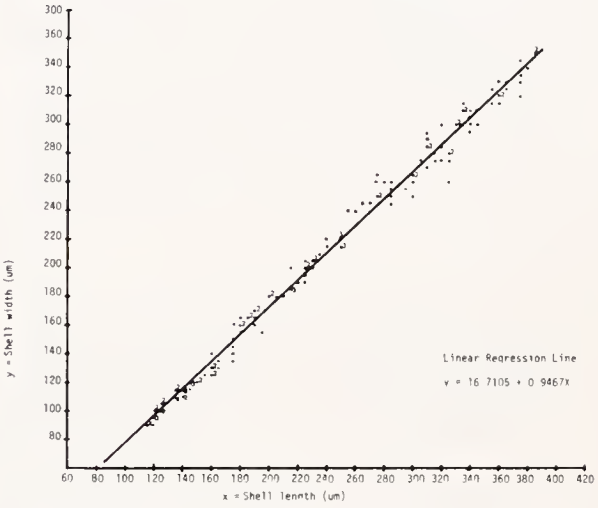


FIGURE 3. *Length - width relationship of geoduck larvae.*

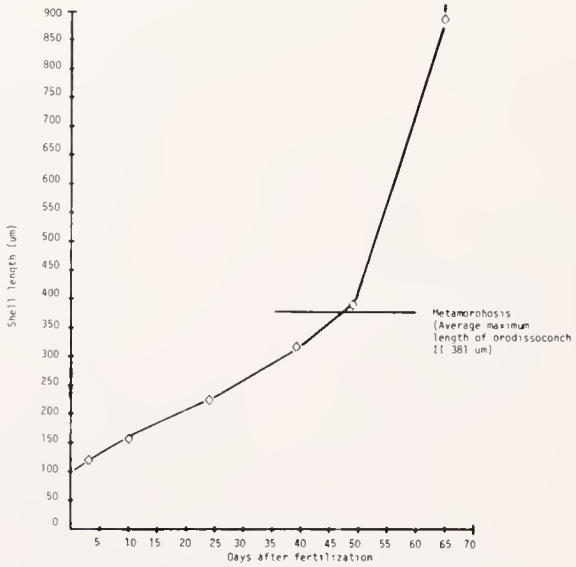


FIGURE 4. *Growth of geoduck larvae and post-larvae. Cultured at 14-15 C. Each dot represents the mean length of 20 larvae randomly chosen.*

their swimming ability at 350 μm and in other cultures larvae as rge as 400 μm, can still swim. Savage and Goldberg (1976) defined metamorphosis as the loss of the swimming functions of the velum. Prior to loss of the velum, the larvae may spend considerable time on or near the bottom of the containers even in apparently healthy unstressed cultures.

The post-larvae are very active crawlers and have a foot that can be extended more than the length of the shell. The dissoconch shell is covered by prominent spines which are common in other hiatelid clams (Savage and Goldberg, 1976). The spines begin along a distinct line in the shell between the prodissoconch 11 and the dissoconch and are easily distinguished in postlarval shells (Figure 2).

LITERATURE CITED

Andersen, A. M., Jr. 1971. Spawning, growth, and spatial distribution of the geoduck clam, *Panope generosa*, Gould, in Hood Canal, Washington. Ph.D. Thesis, Univ. of Wash., Wash. Coop. Fish. Unit 133 p.

Goodwin, L. 1973. Effects of salinity and temperature on embryos of the geoduck clam (*Panope generosa*, Gould). Proc. Nat. Shellfish Assoc. 63: 93-95.

Goodwin, C. L. 1975. Observations on spawning and growth of subtidal geoducks (*Panope generosa*, Gould). Proc. Nat. Shellfish Assoc. 65: 49-58.

Loosanoff, V.L. and H. C. Davis. 1963. Rearing of bivalve mollusks. p. 1-136: Advances in Marine Biology. Ed. F.S. Russel. Acad. Press, London.

Loosanoff, V. L., H. C. Davis and P. E. Chanley. 1966. Dimension and shapes of larvae of some marine bivalve mollusks. Malacologia 2: 351-435.

Savage, N. B. and R. Goldberg. 1976. Investigation of practical means of distinguishing *Mya arenaria* and *Hiatella sp* larvae in plankton samples. Proc. Nat. Shellfish Assoc. 66: 42-53.

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OBSERVATIONS ON THE MOLT CYCLES OF TWO SPECIES OF JUVENILE SHRIMP, *PENAEUS CALIFORNIENSIS* AND *PENAEUS STYLIROSTRIS* (DECAPODA: CRUSTACEA)[1, 2]

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ABSTRACT

The molt cycles of two species of juvenile (90-107 days old) penaeid shrimp, Penaeus californiensis *(a "grooved" shrimp), and* Penaeus stylirostris *(a "non-grooved" shrimp), were studied. Duration of the intermolt periods and various molt stages were comparable. A description of the various molt stages for penaeid shrimps is presented. It is based on progressive changes in the morphology of uropod setae and relative hardness of the exoskeleton. Progressive changes in the appearance of setae during the molt cycle were consistent with reports in the literature for both heavily mineralized Reptantian and lightly mineralized Natantian decapod crustaceans. Both species were difficult to handle and their behavior, which differed greatly, is discussed.*

INTRODUCTION

Penaeid shrimp support important commercial fisheries in temperate, subtropical, and tropical regions of the world. However, declining catches and rising prices have led to increasing interest in the mariculture of these shrimp.

Shrimp must periodically molt in order to grow. For juveniles, this continuous process is interrupted only by unfavorable environmental conditions or maturity (Norvales et al., 1973). Immediately after the molt they are very vulnerable and may fall prey to non-molting shrimp at the high densities of intensive culture. This consideration led Segal and Roe (1975) to conduct an extensive study of molting frequency of the prawn, *Macrobrachium rosenbergii*, held at several densities with varied social structures.

The crustacean molt cycle is divided into soft (A), postmolt (or paper shell) (B), intermolt (C), premolt (D), and molt (E) (Passano, 1960). Procedures for identifying molt stages of Natantians other than the penaeids are well documented (Scheer 1960; Drach and Tchernigovtzeff, 1967), and have been employed by several investigators in studies of lipid metabolism of *Penaeus japonicus* (Kanazawa et al., 1972; Kanazawa et al., 1975; Kanazawa et al., 1976) and of the responses of *Penaeus californiensis* to varied dietary Ca:P ratios (Huner and Colvin, 1977). However, there are no descriptions, to our knowledge, of the molt stages and their duration of any species of penaeid shrimp including either

1 This work was supported, in part, by a grant from the Coca-Cola Company, Atlanta, Georgia.
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of the two major categories, the so-called "grooved" and "non-grooved" species. There are at least two reasons for this situation. First and foremost, such shrimp are extremely sensitive to handling trauma and frequently develop terminal conditions such as "cramped" shrimp and "spontaneous necrosis" (Johnson, 1975) after being removed from the water and manipulated for very brief periods— less than two or three minutes. Second, only within the past decade have there been any really concentrated efforts to culture such species with the resultant need to obtain descriptive information about their molt cycles.

This study was initiated to obtain baseline, comparative data on the molt cycles of two species of juvenile, penaeid shrimp, *Penaeus californiensis* (a "grooved" shrimp) and *Penaeus stylirostris* (a "non-grooved" shrimp). Both species are now under investigation as potential candidates for intensive culture.

MATERIALS AND METHODS

The investigations, conducted at the controlled environment aquaculture facility in Puerto Penasco, Sonora, Mexico, employed two groups of *P. californiensis*, 90 days old — 0.59 g mean initial weight and 96 days old — 1.97 g mean initial weight, and one group of *P. stylirostris*, 107 days old — 2.45 g mean initial weight. Shrimp were held individually in cylindrical cages (17 cm diameter x 40 cm height) constructed of 0.6 cm mesh DuPont Vexar^{R} material. Six *P. californiensis* or five *P. stylirostris*, were placed in 50 x 50 cm^2 fiberglass tanks maintained at a water depth of 10 cm. Each tank was equipped with an airstone and received a continuous flow of seawater (from a 20 m well) with 8-10 exchanges per day. Observed water quality parameters included: dissolved oxygen, at or near saturation; temperature, 22.6° ± 1°C; salinity, 32 ± 1 ppt; and pH, 7.6 - 8.0. The photophase was slightly longer than that of the natural photoperiod (July-August) with occasional interruptions during the scotophase. All shrimp were fed at a daily rate of 10% of initial mean body weight with a routine maintenance diet having the following proximate composition(%): protein, 29.6; fat, 3.5; fiber, 4.7; gross energy, 3.9 Kcal/g; calcium, 2.8; and phosphorous, 1.0.

Twenty-four *P. californiensis* of each size (48 total shrimp) were randomly distributed into each of four tanks and were examined for molt stage once every three days. Six shrimp of each size (12 total shrimp) served as unhandled controls. They were not disturbed other than for normal tank cleaning.

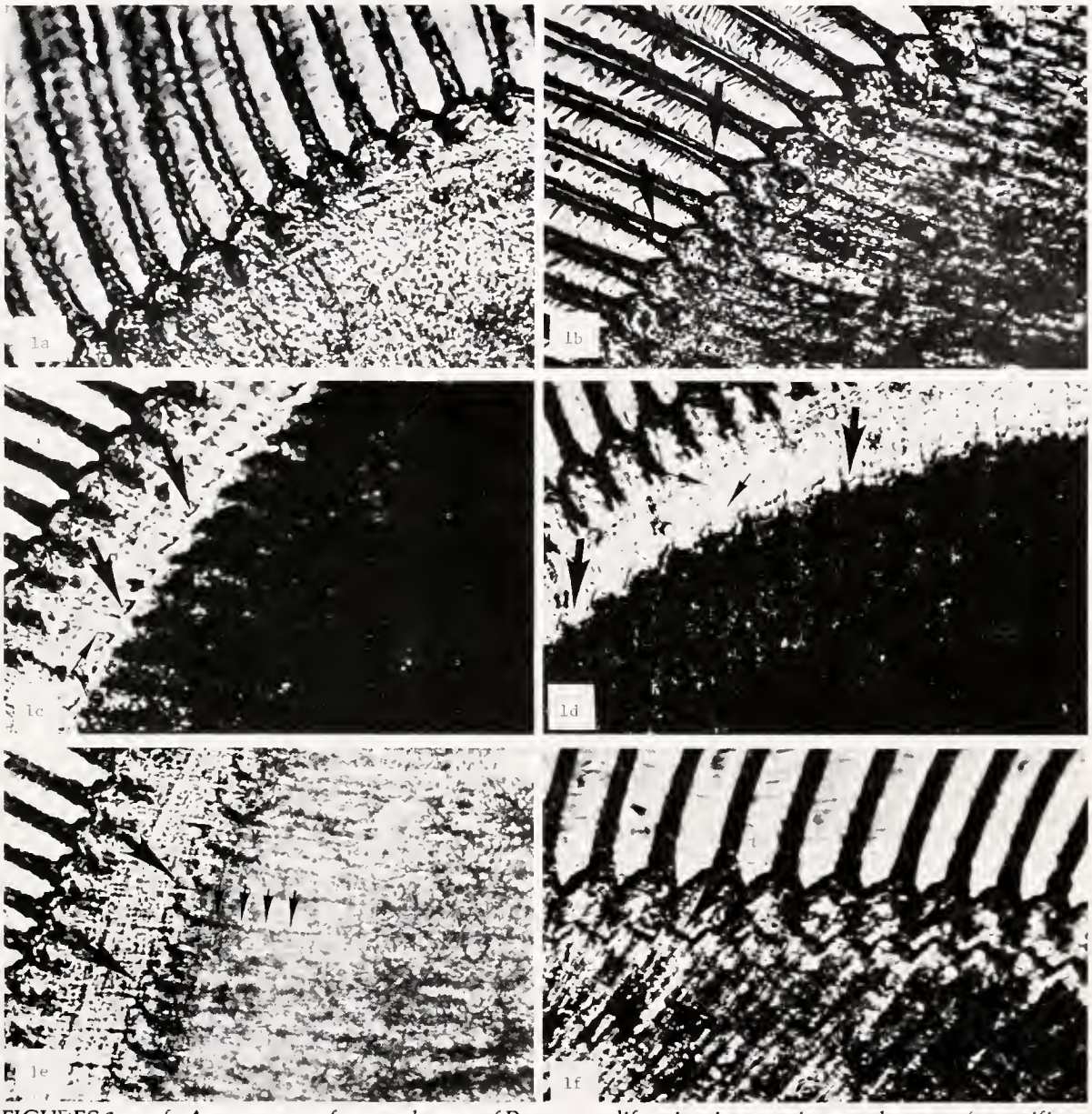
Twenty *P. stylirostris* were distributed five per tank and were examined for molt stage every three days. There were no unhandled controls.

Molt stage for shrimp used in this study was determined by microscopic observation at 100 magnification of new setae at the edges of uropods and by noting progressive changes in the relative hardness of the carapace (Drach and Tchernigovtzeff, 1967; Stevenson, 1972; Aiken, 1973).

Since both species were very sensitive to handling, the following procedure was employed to minimize trauma. Each shrimp was removed from its cage and carried to the examination table in an individual container of water. The shrimp was removed from the water; the anterior half covered with a wet paper towel; and the uropods examined. Following examination, which required no more than 25-30 seconds, the shrimp was returned to its cage.

Stage A (recently molted) shrimp were not handled. We could not easily differentiate between stages B and C during the initial phase of our work. Therefore, emphasis was placed on the premolt stage (D) of the cycle since it normally occupies 60% of the molt cycle of most crustaceans (Passano, 1960) and we could separate substages with relative confidence.

We arbitrarily divided the premolt stage into three periods, D_0, D_1(including D_0^{I}, D_1^{II}, D_1^{III}), and, D_{2+}, because observation of shrimp at three day intervals, rather than on consecutive days, and the rapid molting rate did not permit finer analysis. When using progressive changes in body setae as criteria for differentiating molt stages, the substages D_0, D_1^{I}, D_1^{II}, D_1^{III}, and D_2 are as described by Scheer (1960), Drach and Tchernigovtzeff (1967), Stevenson (1972), and Aiken (1973). Substage D_0 is marked by retraction of epidermis from the bases of the setae. Stage D_1 begins (D_1^{I}) with indentation of retracted epidermal tissue and ends (D_1^{III}) with completion of new setae as "tubes within tubes" but without



FIGURES 1a — f. *Appearance of uropod setae of* Penaeus californiensis *at various molt stages (magnification = 100 X).*

Legend — 1a. Stage B; 1b. Stage C. Note well formed inner cones at the bases of setae (see arrows); 1c. Substage D_0. Note: (1) Retraction of epidermis at the bases of old setae (large arrows) and (2) setal organs which are perpendicular to the retracting epidermis (small arrow); 1d. Substage D_1^I. Note: (1) Columnar appearance of the edge of the retracted epidermis (large arrows) and (2) well formed setal organs (small arrows); 1e. Substage D_1^{III}. Note the "tube within tube" appearance of new setae. Large arrows show two new setae and small arrows show lateral demarcation between two setae; 1f. Substage D_{2+}. Note that new setae occupy most of the space within the old uropod. They have a very dense, opaque appearance because of extensive development of lateral barbules on their central shafts. Arrows point to the distal ends of two new setae.

TABLE 1. *Description of variation in the morphology of uropod setae and of changes in exoskeleton strength for two species of penaeid shrimp,* Penaeus californiensis *and* Penaeus stylirostris.

Stages A, B, C[1]	No retraction of epidermis is apparent at the bases of uropod setae (figs. 1a, 1b, 1c).
Stages A & B	Inner cones just above the bases of the new setae are not developed (fig. 1a).
Stage A	Fluid may be seen flowing through the shafts of the new setae in live shrimp. The exoskeleton is very soft to slightly rigid (parchment-like).
Stage B	No fluid may be seen flowing through the shafts of the new setae in live shrimp. The exoskeleton is slightly rigid (parchment-like).
Stage C	Inner cones just above the bases of the new setae are well developed (fig. 1b). The exoskeleton is as rigid as it will become but remains flexible.
Stage D	Retraction of the epidermis is apparent at the bases of the uropod setae (figs. 1c, 1d, 1e, 1f).
Substages D_0 & D_1	The shell remains as rigid as it was during Stage C.
Substage D_0	The edge of the retracted epidermis is smooth without distinct shape. After retraction becomes fully apparent, narrow, pointed setal organs can be seen projecting from this edge. These persist into Substage D_1 when invagination along their edges gives rise to the central, distal shafts of the new setae (fig. 1c).
Substage D_1^{I}	The edge of the retracted epidermal tissue has distinct definition (columnar shape) but there is no evidence of extensive invagination distal to the edge (fig. 1d).
Substage D_1^{II}	There is evidence of invagination distal to the edge of the retracted epidermal tissue as new setae form.
Substage D_1^{III}	Invagination is complete and new setae are formed appearing as "tubes within tubes." The bases of the new setae have no distinct end. Lateral barbules are seen forming along the distal tip of the central shafts of the new setae (fig. 1e).
Substages D_2, D_3, & D_4	The old exoskeleton becomes progressively more brittle and the new exoskeleton can be separated from the old one.
Substage D_2	The bases of the new setae have a distinct, inverted V shape. Barbule development on the central shafts of the new setae reaches its maximum extent (fig. 1f).
Substage D_3	The bases of the new setae have a distinct, rounded shape.
Substage D_4	A narrow separation appears between the carapace and the abdomen.

[1]In general, the following Stages A, B, C, and D are referred to as Soft (A), Postmolt (B), Intermolt (C), and Premolt (D). The actual molt is referred to as Stage E. The molting process was described for crayfishes by Aiken (1968) and appears virtually identical for penaeid shrimps. A brief description of the substages of Stage E follows.

Stage E	The molt itself.
Substage E_1	The thoraco-abdominal membrane is distended and the posterior margin of the carapace is slightly elevated.
Substage E_2	The carapace is thrown forward, and the cephalic structures are withdrawn.
Substage E_3	The abdomen and related components are withdrawn.
Substage E_4	The walking legs are withdrawn and the shrimp flips free of the old exoskeleton.

extensive formation of lateral barbules on the central shafts. Progressive formation of lateral barbules marks substage D_2 and subsequent premolt substages.

The three day examination interval was chosen because we felt that it would permit normal molting while shorter intervals might have impeded molt because of handling trauma. There were no significant differences ($P<0.05$) between handled versus unhandled controls of *P. californiensis* with respect to duration of the intermolt period. Space limitations precluded use of unhandled controls for *P. stylirostris*.

Subsequent to the observations made in the original series of experiments, we were able to discriminate between molt stages B and C by the presence (stage C) or absence (stage B) of setal cones at the bases of the uropod setae (Figures 1a and 1b). Table 1 provides a description of the changes observed in uropod setae during the entire molt cycle with emphasis on stage D since histological studies are required to separate substages of stages A, B, and C. Similar changes occur in all setae but morphological differences in setae make appearance somewhat different.

RESULTS AND DISCUSSION

Molting and Growth

The duration of the intermolt period of the younger/smaller *P. californiensis* was 7.4 ± 0.2 days (n = 78) with a range of 5 to 10 days (mode, 7 days, n = 27). The older/larger *P. californiensis* had a mean intermolt period of 11.8 ± 0.7 days (n = 37) with a range of 7 to 15 days (modes, 10 and 13 days, n = 8). The mean intermolt period of *P. stylirostris* was 9.1 ± 0.6 days (n = 17) with a range of 7 to 11 days (modes, 8 and 9 days, n = 5).

The younger/smaller *P. californiensis* molted at a much more rapid rate than did the slightly older/larger shrimp of either species, but when shrimp of similar sizes were compared, *P. stylirostris* molted most rapidly. However, growth of the two groups of larger shrimp was comparable; that is, percentage increase in weight per molt was 29% and 27% for *P. californiensis* and *P. stylirostris*, respectively (Table 2). The growth rate of the smaller *P. californiensis* was almost twice that of the larger shrimp, i.e., 46% increase in weight per molt.

The initial differences in ages between the younger *P. californiensis* and the older *P. californiensis* and *P. stylirostris* were not great; however, the differences in sizes were pronounced. The younger *P. californiensis* had been held at densities roughly twice those of the larger shrimp of either species prior to beginning the experiments. We feel that the rapid molting rate and marked growth increment per molt of the younger shrimp reflected the compensatory growth phenomenon frequently observed when organisms are placed in a favorable environment after having been in an unfavorable one for a time.

Reduced food consumption was noted in all treatments involving the larger shrimp. All shrimp were observed to discontinue feeding for a period

TABLE 2. *Comparative growth data for juvenile* Penaeus californiensis *and* Penaeus stylirostris.

Species	Initial Age (days)	Initial Wt (g)	Final Wt (g)	% Increase in Wt/Molt[1]	Molts/Shrimp
P. californiensis	90	0.59 ± 0.04 (n=29)	1.54 ± 0.09 (n=30)	46 (n=30)	3.6 ± 0.2[2] (n=98)
P. californiensis	96	1.97 ± 0.20 (n=30)	3.15 ± 0.25 (n=30)	29 (n=30)	2.2 ± 0.2[2] (n=64)
P. stylirostris	107	2.54[4] (n=20)	3.19 ± 0.60 (n=18)	27[4]	1.9 ± 0.2[3] N=52)

[1]Based on initial weight.
[2]Experimental period=27 days.
[3]Experimental period=14 days.
[4]These shrimp were group weighted initially; therefore, composite values, only, could be used as indicated.

between 12-24 hours before and 6-12 hours postmolt with the period of no feeding being greater for larger shrimp. In addition, it was noted that if feed remained in the water for more than 3-4 hours, shrimp would not eat it even if they had resumed feeding following molt. Exuivae were also removed; however, in the case of smaller shrimp these were more often partially consumed when discovered. This probably involved more rapid resumption of feeding of the smaller shrimp. Therefore, more "food" was "lost" to larger shrimp than to smaller shrimp by removing exuivae. In communal systems, we have noted that virtually all food is consumed since nonmolting shrimp will eat food not consumed by molting shrimp.

Molt Stages and Their Duration

Descriptions of molt stages in Table 1 are based on our observations of changes during the molt cycles of *P. californiensis* and *P. stylirostris* as compared to available literature (Scheer, 1960; Drach and Tchernigovtzeff, 1967; Stevenson, 1972; Aiken, 1973; Mills and Lake, 1975; Peebles, 1977). Figures 1a-1f are from different molt stages of *P. californiensis*. The basic appearance is the same for both species; however, the setae of *P. stylirostris* are narrower than those of *P. californiensis* and background pigmentation differs for the two species.

We could discern no major differences between available descriptions of molt stages and our own observations. To be certain, setae from different body parts (uropods, pleopods, or antennal scales) are morphologically distinct, but retraction of the epidermis from the old exoskeleton, formation of new setae as "tubes within tubes", and subsequent development of setal cones following molt were consistent between taxa.

These observations are, of course, interesting from the standpoint of comparative physiology since other descriptions of molt stages are based on both heavily mineralized Reptantians and lightly mineralized Natantians. In addition, the similarity between the molt stages of the "grooved" and "non-grooved" penaeids is noteworthy.

Table 3 presents data on the number of days from observation of a premolt substage until molt for the three groups of shrimp. It can be seen that the duration of successive substages decreases markedly as molt approaches, which is common for all crustaceans (Passano, 1960). The premolt stage occupied 64% and 60% of the intermolt cycle for the smaller and larger *P. californiensis*, respectively, and 53% for *P. stylirostris*.

Substage D_0, described as "true" intermolt (Aiken, 1973) or "fail safe" period (Huner and Avault, 1976), may be maintained indefinitely in unfavorable conditions, and was found to be prolonged in both species. It was most pronounced in the larger *P. californiensis* which had the longest intermolt period of all groups studied. These observations suggest that the arrested D_0 substage may be a useful diagnostic tool to bring to a culturist's attention an adverse environmental fac-

TABLE 3. *Mean time from observation of a premolt substage until molt for juvenile* Penaeus californiensis *and* Penaeus stylirostris.

Species	Substage		
	D_0	D_1	D_{2+}
P. californiensis[1]	4.7 ± 0.4 days (n=41)	2.8 ± 0.2 days (n=41)	1.2 ± 0.1 days (n=40)
P. californiensis[2]	7.1 days ± 0.6 days (n=34)	3.9 ± 0.3 days (n=36)	1.4 ± 0.2 days (n=30)
P. stylirostris[3]	4.8 ±0.3 days (n=21)	2.3 ± 0.3 days (n=16)	1.2 ± 0.2 days (n=21)

[1]Initial age = 90 days; initial size = 0.59 g.
[2]Initial age = 96 days; Initial size = 1.97 g.
[3]Initial age = 107 days; Initial size = 2.45 g.

tor(s) in his system. The culturist would then have to identify and correct that factor(s).

As mentioned above, we did not specifically determine the duration of molt stages A, B, and C in this study. However, in a concurrent study, we (Huner et al., 1979) studied postmolt mineralization of 2-4 g *P. californiensis* from molt to 96 hours postmolt. By measuring changes in calcium levels as well as observing progressive histological changes in exoskeleton sections, we found that stage A lasted 6-10 hours and stage B lasted 14-18 hours. The onset of premolt substage D_0 was apparent in some shrimp at 96 hours postmolt. Thus, the duration of stage C is approximately 3-5 days in rapidly growing shrimp.

Comparative Behavior

The behavior of the two species of shrimp differed considerably. When *P. stylirostris* were placed in a container, they reacted violently with exaggerated tail flexures; whereas, *P. californiensis* were much less animated. When the *P. stylirostris* were removed from the water, they were quite docile and permitted considerable handling without violent escape behavior. Conversely, when *P. californiensis* were removed from the water, they were always animated, difficult to secure, and sometimes became quite erratic when returned to the transfer container. Following determination of molt stage, approximately 20% of the *P. californiensis* could be expected to show some sign of "shock" characterized by rigidity and no movement of the appendages, and would often sink to the bottom before resumption of activity. *P. stylirostris* never seemed to have been affected by the examination period, although violent escape behavior was much less pronounced when they were returned to the transfer container.

These general behavior patterns have been also noted when the two species were removed from communal culture systems to obtain growth data. Such differences may reflect variation between "grooved" and "non-grooved" species of penaeid shrimps.

In certain nutrition studies it is initially preferable to study shrimp in isolation to eliminate social problems when attempting to identify true genetic differences in performance. This necessitates periodic examination. In this study we found that both *P. californiensis* and *P. stylirostris* reacted quite violently but differently to periodic handling. It would appear advisable to keep such handling to a minimum.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Aiken, D. E. 1968. Subdivisions of stage E (ecdysis) in the crayfish, *Orconectes virilis*. Can. J. Zool. 46: 153-155.

Aiken, D. E. 1973. Proecdysis, setal development and molt prediction in the American lobster *(Homarus americanus)*. J. Fish. Res. Bd. Can. 30: 1337-1344.

Drach, P. and C. Tchernigovtzeff. 1967. Sur la methode de determination des stades d'intermue et son application generale aux crustaces. Vie et Milieu. Ser. A., Biol. Marine 18: 595-610.

Huner, J. V. and J. W. Avault, Jr. 1976. The molt cycle of sub-adult red swamp crawfish *(Procambarus clarkii* (Girard)). Proc. World Mariculture Soc. 7: 267-273.

Huner, J. V. and L. B. Colvin. 1977. A short term study on the effects of diets with varied calcium: phosphorous ratios on the growth of juvenile shrimp, *Penaeus californiensis* (Penaeidae: Crustacea): A short communication. Proc. World Mariculture Soc. 8: 775-778.

Huner, J. V., L. B. Colvin, and B. L. Reid. 1979. Postmolt mineralization of juvenile California brown shrimp, *Penaeus californiensis* (Decapoda: Penaeidae). Comp. Biochem. Physiol. 62A:889-893.

Johnson, S. K. 1975. Handbook of shrimp diseases. Texas Agricultural Extension Service, Texas A & M University, College Station, Publication No. TAMU SG-75-603, 19 pp.

Kanazawa, A., N. Tanaka, and K. Kashiwada. 1972. Nutritional requirements of prawn — IV. The dietary effect of ecdysones. Bull. Jap. Soc. Sci. Fish. 38: 1067-1189.

Kanazawa, A., S. Teshima, and Y. Sakamoto. 1975. Utilization of dietary cholesterol during

the molting cycle of prawn. Bull. Jap. Soc. Sci. Fish. 41: 1185-1189.

Kanazawa, A., J. B. Gurary, and H. J. Ceccaldi. 1976. Metabolism of ^{14}C sitosterol injected at various stages of the molting cycle in prawn *Penaeus japonicus* Bate. Comp. Biochchem. Physiol. **54B**: 205-208.

Mills, B. J. and P. S. Lake. 1975. Setal development and moult stage in the crayfish, *Parastacoides tasmanicus* (Erichson), (Decapoda Parastacidae). Aust. J. Mar. Freshwater Res. 26: 103-107.

Norvales, R. R., L. I. Gilbert, and F. A. Brown, Jr. 1973. Endocrine mechanisms. In: C. L. Prosser (Editor), Comparative Animal Physiology, W. B. Saunders, Philadelphia, pp. 857-908.

Passano, L. M. 1960. Molting and its control. In: T. H. Waterman (Editor), The Physiology of the Crustacea, Academic Press, New York, pp. 473-536.

Peebles, J. B. 1977. A rapid technique for molt staging in live *Macrobrachium rosenbergii*. Aquaculture **12**: 173-180.

Scheer, B. T. 1960. Aspects of the intermolt cycle in Natantians. Comp. Biochem. Physiol. **1**: 3-18.

Segal, E. and A. Roe. 1975. Growth and behavior of post juvenile prawns *(Macrobrachium rosenbergii* de Man) in close confinement. Proc. World Mariculture Soc. 6: 67-88.

Stevenson, J. R. 1972. Changing activities of the crustacean epidermis during the molting cycle. Am. Zool. **12**: 373-380.

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SHELL LENGTH AT SEXUAL MATURITY OF SURF CLAMS, *SPISULA SOLIDISSIMA*, FROM AN INSHORE HABITAT

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ABSTRACT

Sexual maturity was determined in small surf clams, Spisula solidissima *(Dillwyn), of a discrete group found at Chincoteague Inlet, Virginia, in late 1964. Gametes were present in 12% of the clams in an October 1964 sample, but larger and smaller immature specimens predominated. Most (91%) of the clams in a May 1965 sample were ripe, but, thereafter, differentiated gametes were in only 10% of the samples during the remainder of the year. The few sexually mature clams were the largest or nearly the largest (69 mm or more) in the samples. Although a spawning occurred in early summer of 1965, and some individuals were recognized as sexually mature afterwards, the clams that year were considered not fully mature. Full maturity, characterized by extensively proliferated gonadal tubules and differentiated gonia, was attained by all clams in 1966. The smallest fully mature clam was 45 mm long, but growth to a size larger than other clams in a sample seemed important in earlier development of sexuality. Factors affecting rapid growth, and not age alone, then, seemed to influence attainment of sexual maturity.*

INTRODUCTION

Sexual maturity is attained by an animal when gametes are produced for the first time in its life history. In pelecypods, determination of attainment of sexual maturity is usually hampered by the lack of development of different secondary sexual characteristics. The primary sexual characteristic is the production of distinctly different gametes in the gonadal tissues, but the gametes are usually minute, requiring special procedures to distinguish the cellular differences of each sex. In some species, of which the sea scallop (*Placopecten magellanicus*) is notable, the male and female gonads are differently colored (Posgay and Norman, 1958; Naidu, 1970). In surf clams (*Spisula solidissima*), the ripe ovaries of females are sometimes pink, but may also be white, as are the male testes (Schechter, 1941). Parasites sometimes fill the gonads of surf clams, adding a confounding factor to accurate color observations (Ropes, 1968a). External organs on the soft body of surf clams are minute genital papillae of similar shape and size for both sexes (Stickney, 1963). Secondary sexual characteristics, such as differently colored or shaped shells, to distinguish the sexes of pelecypods are generally absent,

although there are a few exceptions (Cox, 1969). For these reasons, it is necessary to microscopically examine slide preparations of gonadal tissues collected during the period of sexual differentiation (Coe, 1943a, b; Coe and Turner, 1938; Loosanoff, 1937).

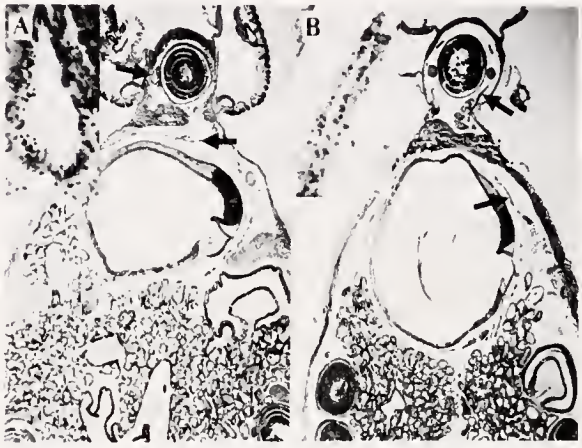
A settlement of surf clams from a spawning in 1964 was discovered in the surf zone of beaches at Chincoteague Inlet, Virginia, on 1 October 1964. Settlement in years before 1964 had apparently not been successful, because shell length measurements were easily distinguishable as a discrete group during 40 months of observation. Other sets of surf clams occurred in late 1966 and 1967, but these clams were easily separated by their smaller size, lack of overlap in the size frequency measurements with those of the 1964 "year class", and smaller number of individuals[1]. Collections of this 1964 "year class" were made on many occasions until early 1968 for marking experiments (Ropes and Merrill, 1970). Specimens from the earliest samples through those in 1965 and 1966 were used in the following study of size at sexual maturity.

SAMPLE COLLECTION AND METHODS

The sample size of clams collected at Chincoteague Inlet varied, but the average number taken for measurements of shell length was often large (200-500); clams used for an examination of sexual maturity included specimens differing in length by 11 to 54 mm. All shell length measurements were made to the nearest millimeter with calipers. Histological preparation of gonadal tissues for microscopic examination and identification of phases of gonadal condition follow the description given by Ropes (1968a). Except for one collection on 12 May 1965 which was stored in 70% ethanol, Bouin's was used to fix all of the tissues.

GONADAL HISTOLOGY AND DETERMINATION OF SEXUAL MATURITY

A description of gonadal histology and comparison with other species is necessary to develop criteria for determining sexual maturity in the surf clam. The gonads of surf clams originate from cells located in the posterior portion of the body, near the visceral ganglion and below the pericardium. Multiplication of the primordial germ cells results in more or less separate follicles on each side of the body (Figure 1). The branching tubular follicles grow anteriorly, surround the intestine and crystalline style sac, and eventually overlay the digestive diverticula.



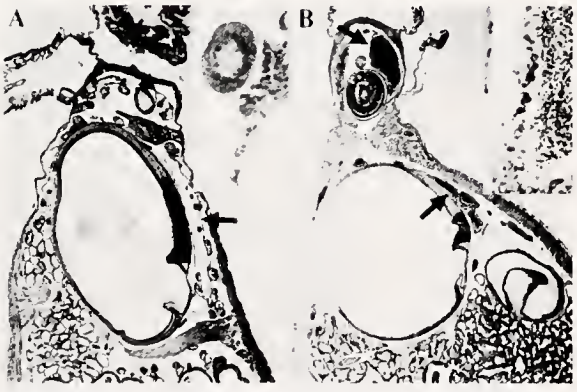
(FIGURE 1.) *(A) and (B). Sections of immature surf clams,* Spisula solidissima, *collected on 1 October 1964 at Chincoteague Inlet, Virginia. Both were 26 mm long. Arrows point to gonadal tubules. Enlargements in the upper-left corners are of tubules and primary gonia. Magnification of whole section 9.75X and of enlargement 2.10X.*

Early gonadal development in surf clams is similar to that in other pelecypods (Coe, 1943a). The gonadal histology in mature surf clams, however, is significantly different than in species he examined. Coe characterized three distinct types of gonads. In one type, exemplified by *Mya arenaria* and *Petricola pholadiformis*, branching tubules contain primary gonia and large vacuolated follicular cells. The latter are accessory nutritive cells which nearly fill the lumina of the tubules and are cytolyzed during gametogenesis. In the second type, exemplified by *Crassostrea virginica* and *Mytilus edulis*, only gonia and a few minute follicular cells are contained within the tubules, and vesicular connective tissue surrounds the tubules. Nourishment of the gametogenic cells is from the latter tissues. In a third type, ex-

[1] Measurement data for these clams are on file at the National Marine Fisheries Service's Woods Hole Laboratory, Woods Hole, Massachusetts, 02543.

emplified by *Anomia simplex*, gonadal tissues are considered intermediate between the other two types. Gonadal follicles contain gametogenic cells alone, and nutritive cells in tissue form surround the follicles. In the surf clam, vacuolated follicular cells within the gonadal tubules or vesicular connective tissue around the tubules were not found in either juveniles or adults. Small cells in the basement membrane of the tubules and scattered around the tubules may function as nutritive cells. Surf clams, then, exhibit an additional type of gonadal tissue to the three described by Coe (1943a). As indicated by the photomicrographs of Calabrese (1970), the gonadal tissues of the mactrid coot clam, *Mulinia lateralis*, like the surf clam, lack follicular cells and connective tissue. Machell and De Martini (1971) found no follicular cells in the gonadal tubules of the mactrid gaper clam, *Tresus capax*, but did find follicular tissue surrounding the tubules. The gonadal tissue type seen in surf clam gonads, then, may not be typical of all mactrid species.

Absence of follicular cells or vesicular connective tissue in surf clam gonads limits criteria for identifying maturity to changes in sex cells and gonadal tubules. Primary oogonia and spermatogonia can be recognized by their larger size than the nutritive cells in the basement membrane,



(FIGURE 2.) *Sections of very early female (A) and male (B) gonadal development in surf clams,* Spisula solidissima, *collected on 1 October 1964 at Chincoteague Inlet, Virginia. The female clam was 29 mm long, the male 24 mm long. Arrows point to gonadal tubules. Enlargements in upper-right corners are of tubules and sex cells. Magnification of whole section 9.75X and of enlargement 210X.*

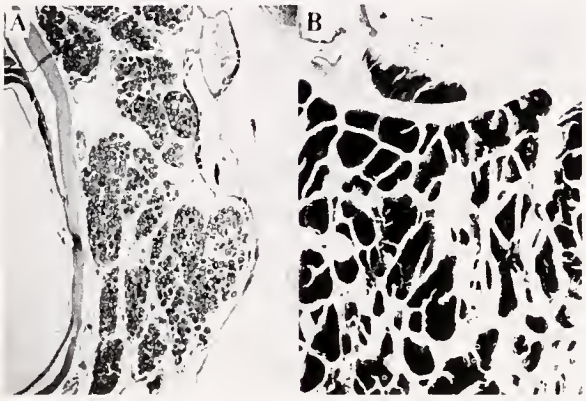
but differentiation between the two types was not possible. Even if it were possible, eventual development of viable sex cells is not assured by the mere presence of the primary gonia in slide preparations. Division of the primary spermatogonia and enlargement of oogonia were thought to be better evidence of maturity, but gonad tubule proliferation to nearly the development seen in large surf clams was an additional and important criterion considered necessary to categorize a specimen as sexually mature.

SAMPLE OBSERVATIONS

Shell lengths of 176 clams from the first collection on 1 October 1964 averaged 26.1 mm and ranged from 18 to 42 mm. Only 3 (12%) of the 25 clams prepared for gonadal examination had oocytes or sperm in the tubules (Figure 2), but the tubules were very poorly developed. Differentiated gametes were not found in the remaining 22 clams, and the few gonadal tubules were composed only of thin basement membranes that held primary gonia and nutritive cells (Figure 1). Based on the criteria given earlier, none of these clams were considered mature. No subsequent samples were taken during 1964 for microscopic examination of gonadal tissues.

A total of 164 clams ranging in length from 16 to 79 mm were examined from collections in March to November 1965 (Table 1). Although none of the clams in the March sample was considered mature, 91% of those on 12 May contained numerous oogonia and sperm and had a greater proliferation of gonadal tubules than had been seen in 1964. They were classified in the ripe gonadal condition (Figure 3). In July and August samples, the gonadal tubules of all clams examined were poorly developed and sexual differentiation was not possible. The absence of differentiated gametes in these clams suggested that a spawning had occurred between mid-May to late July. During the remainder of the year, only occasional clams were classified as mature, because gonia were differentiated and they had extensive gonadal tubules. These mature individuals tended to be the largest clams in a particular sample. In summarizing the observations for 1965, only 9% of all the clams examined were classified as mature, and, thus, a sexually mature condition was not clearly expressed throughout the year.

In 1966, 142 clams were examined from collections in January to October and they were 45 to 85 mm long (Table 1). The gonia were easily differentiated and the tubules were extensive in all of the clams. A progressive ripening resulted in partially spawned and spent individuals in July and August. Sexual maturity was a definite condition of these clams after spawning because numerous easily differentiated gonia were proliferating from the many gonadal tubules.



(FIGURE 3.) *Section of gonadal tubules of surf clams,* Spisula solidissima, *collected on 12 May 1965 at Chincoteague Inlet, Virginia, containing numerous oogonia (A) and sperm (B). The female clam was 51 mm long, the male 42 mm long. Magnification of whole section 9.75X and of enlargement 210X.*

DISCUSSION

My microscopic examinations of *Spisula solidissima* provide evidence and support for the statements by Belding (1910) that surf clams one year old (ca 39 mm) can produce spawn, but have the first important spawning in the second year of life (ca 67 mm).

Certain facts already known about *Spisula solidissima* can be related to the size attained at sexual maturity. This mollusc is one of the largest pelecypods inhabiting the continental shelf along the east coast of North America—only the Atlantic deep-sea scallops, *Placopecten magellanicus,* may be as large or larger. Ropes, Chamberlin, and Merrill (1969) reported a maximum shell length of 210 mm for the surf clam; Ropes and Ward (1977) reported 226 mm. The smallest clam classified as mature in 1966 was 45 mm long and had attained one-fifth the maximum size for this species. In a study of the horse clam, *Tresus capax,* a Pacific coast species in the same family Mactridae as the

CHINCOTEAGUE INLET

DATE	MATURE CLAMS								IMMATURE CLAMS		
	SEXED AS		GONAD CONDITION					RANGE of SHELL LENGTHS	NUMBER in SAMPLE	RANGE of SHELL LENGTHS	TOTAL CLAMS in SAMPLE
	MALE Percent	FEMALE Percent	EARLY Percent	LATE Percent	RIPE Percent	PtSPAWN. Percent	SPENT Percent	mm	Percent	mm	Number
1965											
17 Mar.	0	0	0	0	0	0	0	0	100	19-41	14
12 May	55	36	0	0	100	0	0	33-51	9	32	11
28 July	0	0	0	0	0	0	0	0	100	39-50	9
24 Aug.	0	0	0	0	0	0	0	0	100	38-66	24
7 Sept.	0	3	0	100	0	0	0	70	97	16-63	39
22 Sept.	0	0	0	0	0	0	0	0	100	43-78	22
30 Oct.	8	0	0	0	0	100	0	70-75	92	35-76	24
23 Nov.	9	0	0	0	0	100	0	69-79	91	38-72	21
1966											
19 Jan.	39	61	100	0	0	0	0	48-77	0	0	23
22 Mar.	71	29	32	64	4	0	0	45-77	0	0	28
4 May	46	54	11	89	0	0	0	49-85	0	0	39
28 June	45	55	15	85	0	0	0	65-85	0	0	20
18 July	58	42	13	0	0	29	58	60-82	0	0	7
16 Aug.	50	50	50	0	0	0	50	68-79	0	0	10
11 Oct.	100	0	80	20	0	0	0	62-82	0	0	5
12 Oct.	60	40	90	10	0	0	0	65-85	0	0	10

(TABLE 1.) *Gonadal condition of surf clams,* Spisula solidissima, *from Chincoteague Inlet, Virginia, in 1965 and 1966.*

surf clam, Bourne and Smith (1972), concluded that sexual maturity was attained at a shell length of about 70 mm. This is about one-quarter of the 250 mm maximum size given by Abbott (1974) for *T. capax*. Wolfe and Petteway (1968) found that a smaller mactrid, the brackish-water clam, *Rangia cuneata*, in Trent River, North Carolina, reached maximum lengths of 70-75 mm. Although Cain (1972) did not obtain growth data for adult *R. cuneata* in the James River, Virginia, he observed recognizable sex products in 50% of the clams 14-20 mm, or at about one-quarter or less the maximum size. A minute mactrid species, the coot clam, *Mulinia lateralis*, reaches a maximum length of 15-20 mm (Calabrese, 1969). In laboratory experiments, he found sexually mature males and females 2.7 mm long and induced them to spawn viable gametes. This was less than one-fifth the maximum size. For these five mactrids, then, sexual maturity was usually attained after growing to one-quarter the maximum size and even occurred at smaller sizes in some individuals.

Quayle and Bourne (1972) contend that sexual maturity is a function of size rather than age. This observation seems to apply to surf clams. The five specimens with gonads in the late or partially spawned condition in September through November 1965 were among the largest individuals in a sample. Since we believe all of the clams examined were from a discrete settlement, the age of these larger clams was the same as the smaller individuals that were considered immature.

Coe (1943a) has used the terms "juvenile sexuality" and "neoteny" to describe pre-adult phases in the sexual development of *Mercenaria mercenaria* and *Crassostrea virginica*. Individuals of both species exhibit hemaphroditic tendencies which are most often recognized during a pre-adult phase of their life history. In the former species, there can be a functional change in the sexuality of the pre-adults and about 98% are protandric, but the adults are dioecious. Three types of ambisexual conditions other than the true male and true female types were recognized. In *C. virginica* there is also a strong protandric tendency in pre-adults and five types of ambisexual condition other than true male and true female types were recognized. After the second year of life, female oysters are equal in number to males or are in excess. *C. virginica* was given as an example of alternative sexuality; *M. mercenaria* as consecutive sexuality. Important distinctions are that the pre-adult gonads of ambisexual species usually contain differentiated sex cells, but the primary gonad of strictly dioecious species usually contains undifferentiated sex cells and a "juvenile sexual" or pre-adult phase is lacking. The latter seems applicable to the surf clam.

There is little evidence for juvenile sexuality in the collections of surf clams from Chincoteague Inlet. The three specimens in the 1 October 1964 sample containing a few oocytes and some sperm are possible examples, based on the observation by Coe (1943a) that small numbers of gametes may be formed by pre-adult ambisexual species when very young and at a diminutive size. The sex cells of these few individuals were differentiated, but cells indicating ambisexuality were absent; the sex cells for the remaining individuals in the sample were undifferentiated. In addition, it was not possible to differentiate the sex of most of the specimens collected in 1965, and those classified as immature again contained only undifferentiated sex cells. The absence of evidence for ambisexuality in these samples identifies the surf clam as a dioecious species, but hermaphroditism can occur, even though it is rare and an anomalous condition (Ropes, 1968b).

Ambisexual species can exhibit the protandric condition in young individuals and the protogynous condition in older individuals. It is not possible to identify either condition in young surf clams because too few specimens were sufficiently developed sexually in the 1965 samples. In 1966, sex was recognizable in clams from all eight samples and 76 of the 142 clams were males. The hypothesis of a 1:1 ratio of males and females was tested and the differences were not significant ($x^2 = 6.10$; $df = 7$; $P > .5$). Thus, in 1966 neither condition was apparent, a situation that would be typical for a dioecious species.

Development to full sexual maturity in the surf clams at Chincoteague Inlet seemed to be a gradual process rather than an "all-at-once" or "threshold" of attainment. Gametogenesis, which resulted in spawning, was indicated by the many ripe individuals in the May 1965 sample and it is a

matter of conjecture whether the gametes were viable or not, since only morphological features are apparent in slide preparations. Nevertheless, except for a few of the largest individuals, differentiation of sex for most clams in the remaining 1965 samples was not possible. A return to the earlier undifferentiated condition for most of the clams indicated that full sexual maturity had not been attained.

Spent clams are theoretically the most difficult to sex, because gamete development is in the earliest stages and cellular morphological features are more nearly alike. In large mature clams from offshore, a complete evacuation of gametes from the gonads is rarely seen in slide preparations and the few ripe gametes aid in the identification of sex (Ropes, 1968a). The development of primary sex cells is often well underway even in spent individuals, suggesting that successive reproductive cycles overlap one another. Gametes of both sexes were differentiated before, during, and after the July 1966 spawning in the Chincoteague Inlet clams. The recognition of male and female gametes in all clams in 1966 suggests that they had reached a developmental stage comparable to fully mature offshore clams.

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LITERATURE CITED

Abbott, R. T. 1974. American Seashells. Van Nostrand Reinhold Co., New York. 633 pp.

Belding, D. L. 1910. Growth and habits of the sea clam (*Mactra solidissima*). *In:* Rep. Comm. Fish. Game, 1909. Commonwealth of Massachusetts Public Doc. 25:26-41.

Bourne, N., and D. W. Smith. 1972. Breeding and growth of the horse clam, *Tresus capax* (Gould), in southern British Columbia. Proc. Natl. Shellfish. Assoc. 62:38-46.

Cain, T. D. 1972. The reproductive cycle and larval tolerances of *Rangia cuneata* in the James River, Virginia. Ph.D. diss., Univ. Virginia, Charlottesville, Virginia. 121 pp.

Calabrese, A. 1969. *Mulinia lateralis*: molluscan fruitfly. Proc. Natl. Shellfish. Assoc. 59:65-66.

Calabrese, A. 1970. Reproductive cycle of the coot clam, *Mulinia lateralis* (Say), in Long Island Sound. The Veliger 12:265-269.

Coe, W. R. 1943a. Sexual differentiation in mollusks. I. Pelecypods. Quart. Rev. Biol. 18:154-164.

Coe, W, R, 1943b. Development of the primary gonads and differentiation of sexuality in *Teredo navalis* and other pelecypod mollusks. Biol. Bull. 84:178-186.

Coe, W. R., and H. J. Turner. 1938. Development of the gonads and gametes in the soft-shell clam (*Mya arenaria*). J. Morphol. 62:91-111.

Cox, L. R. 1969. General features of Bivalvia. *In:* Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Geol. Soc. Amer., Inc., Part N, (1) Mollusca, (6) Bivalvia:N2-N129.

Loosanoff, V. L. 1937. Development of the primary gonad and sexual phases in *Venus mercenaria* Linnaeus. Biol. Bull. 72: 389-405.

Machell, J. R., and J. D. De Martini. 1971. An annual reproductive cycle of the gaper clam, *Tresus capax* (Gould), in South Humboldt Bay, California. California Fish and Game 57: 274-282.

Naidu, K. S. 1970. Reproduction and breeding cycle of the giant scallop, *Placopecten magellanicus* (Gmelin), in Port au Port Bay, Newfoundland. Can. J. Zool. 48:1003-1012.

Posgay, J. A., and K. D. Norman. 1958. An observation on the spawning of the sea scallop, *Placopecten magellanicus* (Gmelin), on Georges Bank. Limnol. Oceanogr. 3:478.

Quayle, D. B., and N. Bourne. 1972. The Clam Fisheries of British Columbia. Fish. Res. Bd. Can. Bull. 179. 70 pp.

Ropes, J. W. 1968a. Reproductive cycle of the surf clam, *Spisula solidissima*, in offshore New Jersey. Biol. Bull. 135:349-365.

Ropes, J. W. 1968b. Hermaphroditism in the surf clam, *Spisula solidissima*. Proc. Natl. Shellfish. Assoc. 58:63-65.

Ropes, J. W., J. L. Chamberlin, and A. S. Merrill. 1969. Surf clam fishery. *In:* Firth, F. E. (ed.), The Encyclopedia of Marine Resources. Van Nostrand Reinhold Co., New York. Pp. 118-125.

Ropes, J. W., and A. S. Merrill. 1970. Marking surf clams. Proc. Natl. Shellfish. Assoc. 60:99-106.

Ropes, J. W., and G. E. Ward. 1977. The Atlantic coast surf clam fishery—1974. Mar. Fish. Rev. 39(5):18-23.

Schechter, V. 1941. Experimental studies upon the egg cells of the clam, *Mactra solidissima*, with special reference to longevity. J. Exp. Zool. 86:461-477.

Stickney, A.P. 1963. Histology of the reproductive system of the soft-shell clam (*Mya arenaria*). Biol. Bull. 125:344-351.

Wolfe, D. A., and E. N. Petteway. 1968. Growth of *Rangia cuneata* Gray. Chesapeake Sci. 9:99-102.

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SANITARY SIGNIFICANCE OF THE BACTERIAL FLORA OF THE BRACKISH WATER CLAM, *RANGIA CUNEATA*, IN ALBERMARLE SOUND, NORTH CAROLINA

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ABSTRACT

The bacteriology of Rangia cuneata *was studied to assess the sanitary safety in harvesting this clam for human consumption. Standard plate counts fluctuating from tens of thousands to tens of millions per gram were recorded on fresh clam meat. These numbers are relatively high in comparison to levels recorded in other edible shellfish. The bacteriological quality of the clams showed a median fecal coliform count of 80 FC/100 g, but 23% of the samples exceeded 230 FC/100 g. Potentially pathogenic bacteria of the genera* Salmonella, Shigella, Vibrio, *and* Staphylococcus *were recovered at very low levels.*

A statistically significant correlation between clam standard plate counts and incidence of indicator organisms or potential pathogens in clam meats was not observed. The very low of potential pathogens and near compliance with coliform standards indicate that there is no unique threat to public health caused by the bacterial flora of Rangia cuneata. *Large-scale routine coliform testing should be continued to supplement and verify the coliform results reported in this research.*

INTRODUCTION

Rangia cuneata is a brackish water clam found most commonly in the upper reaches of estuaries where the salinity is 0-15°/₀₀. It has long been present in Gulf Coast estuaries and has recently become abundant in Atlantic Coast estuaries from Maryland to Florida (Pfitzenmeyer and Drobeck, 1964; Godwin, 1968; Hopkins and Andrews, 1970). A study by Cain (1975) showed that in one stretch of the James River, Virginia, *Rangia* comprised 95% of the benthic biomass. This clam is an important link in the food chain of oligohaline to mesohaline estuaries, converting detritus to biomass (Darnell, 1958; Tenore et al., 1968). *Rangia* serves as a food source for fish and crustaceans (Suttkus et al., 1954). Cain (1975) cites a report by Wass and Wright that *Rangia* are also a major component in the diet of various waterfowl.

Fossil *Rangia* have been harvested for many years along the Gulf Coast. The shell is used by industry for roadbed and for its chemical content. The use of *Rangia* as a human food source has been reported in a number of localities (Singley, 1893; Speck and Dexter, 1946; Hopkins et al., 1973). Hoese (1972) indicated that a $6 million per year industry could be sustained in a section of southwestern Louisiana if both shell and meat were sold.

Shellfish are filter feeders and are often consumed raw or lightly heated. Therefore, commercial marketing is carefully controlled to protect the public from waterborne disease. This control con-

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sists primarily of the cooperative effort of state regulatory agencies with the National Shellfish Sanitation Program of the Food and Drug Administration which certifies the sanitary quality of the growing-area waters, the shellfish in those waters, and the sanitation of the product processing and marketing.

A growing interest in *Rangia* as a food product has led to scrutiny of its safety from a microbiological standpoint. Between 1966 and 1971 over 300,000 pounds of *Rangia* meat were harvested from North Carolina waters. *Rangia* was marketed in at least two different forms. A breaded product was sold to several motel and restaurant chains both within and outside North Carolina, and reports were made of its excellent flavor (Anonymous, 1964). Large quantities of *Rangia* were canned in ocean clam liquor and sent to a seafood market in New York. The clams were then seasoned, canned in cocktail sauce, and sold as a seafood cocktail. The North Carolina company involved, Willis Brothers Seafood, termed the business "profitable" (Willis Brothers Seafood, 1978).

There were two reasons for termination of the *Rangia* industry in 1972. First, on one occasion a shipment of about 10,000 pounds of clam meat was rejected by public health authorities in New York because of an excessively high standard plate count (Willis Brothers Seafood, 1978). The second and major reason was an extensive closure of *Rangia* growing-area waters in eastern Albemarle Sound by state shellfish sanitation authorities (Chestnut and Porter, 1976). These waters were reopened to shellfishing in October of 1976, and renewed interest in marketing *Rangia* developed.

Our investigation of the clam began through an appeal from the Shellfish Sanitation Program of the North Carolina Department of Human Resources for university research to determine the nature of the bacteriological problem with *Rangia*. Preliminary determinations by that agency indicated the presence of high standard plate counts in North Carolina *Rangia*.

The objective of this research was to study the bacterial flora of the *Rangia* clam and to assess any threat of this flora to public health. Bacterial counts were monitored in clams, water, and sediment taken from Albemarle Sound, North Carolina, to establish the influence of seasonality and other factors on the numbers and kinds of bacteria. This work included enumeration of indicator bacteria as well as screening for potentially pathogenic bacteria.

MATERIALS AND METHODS

Study Area.

Albemarle Sound is an oligohaline estuary located in the northeastern region of North Carolina near the Virginia border (Figure 1). The salinity was characteristically less than 4‰ for most of the year, and surface temperatures ranged from 0-34 °C. There is usually abundant dissolved oxygen at the bottom of the sound, even during the summer months (Bowden and Hobbie, 1977).

Field Collections.

Clam, water, and sediment samples were collected monthly from July 1977 through June 1978 at three stations in Albemarle Sound and one in Roanoke Sound. Stations 1, 2, and 3 were in water

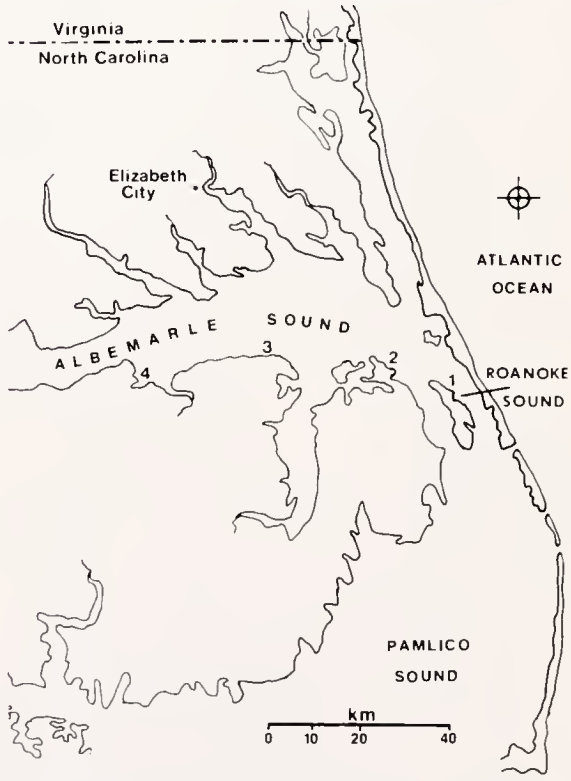

FIGURE 1. *Albemarle Sound, North Carolina. Numbers indicate sampling stations.*

open to shellfishing, and Station 4 was in a closed area (Figure 1). All samples were taken near the shore in water approximately 1 m deep. Clams were collected by raking and were sealed in clean plastic bags. Water samples were obtained in autoclaved polypropylene bottles at a depth of about 0.5 m. Sediment was sampled using chlorine-washed polycarbonate core tubes with an inner diameter of 45 mm. All clam, water, and sediment samples were immediately placed on ice for transport back to the laboratory. In addition to these collections, measurements of air and water temperature, salinity, pH, and dissolved oxygen were recorded at each station.

Laboratory Analyses.

All samples were analyzed for total coliforms (TC), fecal coliforms (FC), and standard plate counts (SPC). The water was also tested for the presence of fecal streptococci (FS). Clam samples were screened for the detection of potential enteric pathogens of the genera *Salmonella, Shigella, Vibrio,* and *Staphylococcus.* This pathogen screening was done for all clam samples except those collected in January. Selected clam samples were stored to simulate market conditions to determine shelf life. Clams were shucked and processed in accordance with recommended methods (APHA, 1970), and dilutions were made in phosphate buffered water. Flow diagrams of the bacteriological analyses performed are depicted in Figures 2 and 3.

Standard plate count.

One ml from the various dilutions of clam, water, and sediment samples was inoculated into standard methods agar (SMA) plates (Figure 2). Bacterial colonies were counted after 48 h and multiplied by the dilution factor to obtain the SPC per gram of clam and sediment or per ml of water.

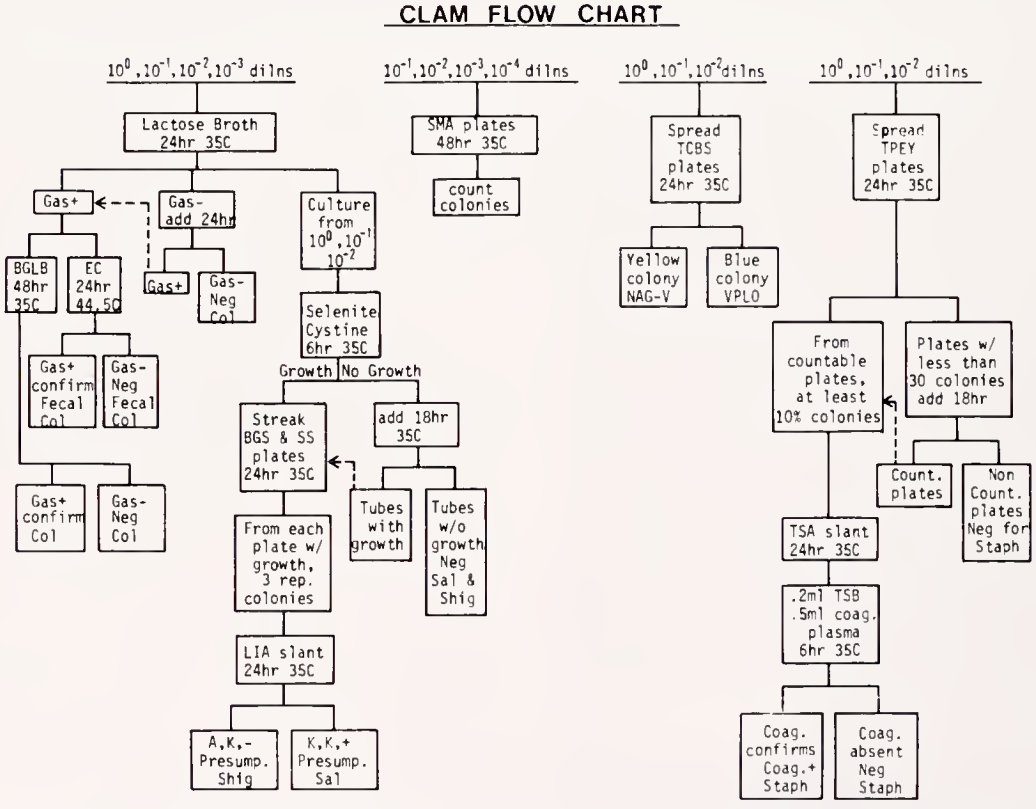

FIGURE 2. *Bacteriological procedures used in analysis of clam meat. Methods were similar for enumeration of indicator organisms in water and substrate, with the addition of fecal strep analysis of water.*

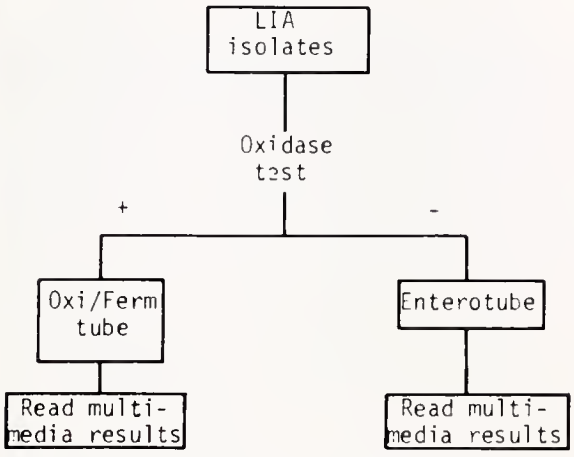

FIGURE 3. *Diagnostic method utilized in confirmation of* Salmonella *and* Shigella.

Indicator organisms.

Standard 5-tube dilution procedures were employed for the determination of a most probable number (MPN) of TC, FC, and FS (APHA, 1975). Lactose broth served as the presumptive coliform medium (Figure 2). Transfers from gas positive tubes were made into brilliant green lactose bile (BGLB) broth for confirmation of TC's and into EC broth for confirmation of FC's. Azide dextrose broth was used as the presumptive and ethyl violet azide (EVA) the confirmatory media for FS enumeration.

Vibrio.

Thiosulfate citrate bile salts sucrose (TCBS) agar was used as the selective medium for enumeration of vibrios (Figure 2). Volumes from the clam homogenate and dilutions equal to 0.1 g, 0.01 g, and 0.001 g were spread on TCBS plates. Consideration was given to using salted buffer dilution water recommended to enhance recovery of *Vibrio parahaemolyticus*. This strategy was rejected because the clams were collected from water that is, for osmotic purposes, essentially fresh (4 ‰). Results of *Vibrio* analyses were recorded as the average count/g. In this system, 1 colony detected on a 0.1 g plate is equivalent to 10 colonies per gram of clam meat. Since there were 4 stations per sample date, the lowest count that could be obtained was 2.5/g. When these bacteria were not detected in a sample, the value recorded was <2.5/g/sample date. Yellow colonies on TCBS were recorded as nonagglutinable vibrios (NAGV). These are vibrios which have the yellow colonial growth on TCBS typical of *V. cholerae*, but do not agglutinate in group 1-0 antigen antiserum. Five of these isolates were sent to the Center for Disease Control (CDC) in Atlanta, Georgia, soon after the first sample date in July 1977. They were confirmed as NAG vibrios. No additional samples were sent to CDC throughout the remainder of the study period due to the volume of samples that agency was receiving from other sources. Blue-green colonies were recorded as *V. parahaemolyticus*-like organisms (VPLO). This is a presumptive enumeration based on the selectivity of the medium.

Staphylococcus.

Plates of tellurite polymyxin egg yolk (TPEY) agar were employed for the enumeration of staphylococci (Figure 2). These plates were inoculated in the same manner as the TCBS plates for *Vibrio* analysis, and enumeration procedures were identical to those used in quantifying vibrios. Representative gray to black colonies were analyzed by coagulase testing, and the number of coagulase positive staphylococci were recorded. These procedures are outlined in *Examination of Foods for Enteropathogenic and Indicator Bacteria* (Lewis and Angelotti, 1964). In the final six months of testing, brain heart infusion (BHI) broth was substituted for Trypticase soy broth (TSB) as growth media during coagulase testing. This was done to adhere more closely to methods recommended in *Bacteriological Analytical Manual* (FDA, 1976).

Salmonella and Shigella

Two procedures were employed at different times in the study for detection of *Salmonella* and *Shigella*. The original scheme, used through December 1977, is both a detection and enumeration method (Lewis and Angelotti, 1964). This scheme (Figure 2) used lactose broth for preenrichment, inoculated quantitatively for enumeration by the multiple tube technique. Transfers were made from lactose broth to selenite cystine, a selective enrichment for *Salmonella* and *Shigella*. Selenite cystine tubes showing growth were used to streak *Salmonella-Shigella* (SS) agar plates for detection of *Shigella* and brilliant green

sulfadiazine (BGS) plates for growth of *Salmonella*. One or two representative colonies were then streaked and stabbed into lysine iron agar (LIA) slants. Butt and slant reactions and H_2S production were recorded in that order as acid (A) or alkaline (K) and $\pm H_2S$ production. Readings of K, K, + were recorded as presumptive *Salmonella* and A, K, - as presumptive *Shigella*. Each of the original lactose broth tubes were then recorded as positive or negative for the presence of *Salmonella* and *Shigella*, and an MPN was determined.

By December 1977, only one presumptive *Salmonella* and no *Shigella* had been recorded. Therefore, beginning in February 1978, a procedure which is more sensitive for detection but does not permit enumeration was adopted (FDA, 1976). In this procedure additional clams were shucked and homogenized directly in selenite cystine enrichment broth. This reduces overgrowth of *Salmonella* and *Shigella* by other bacteria that can occur in lactose broth.

From the selenite cystine pre-enrichment, a variety of agar plates were streaked-bismuth sulfite (BS), SS, and BGS for *Salmonella* culture and xylose lysine desoxycholate (XLD), desoxycholate-citrate (DC), and Levine eosin methylene blue (L-EMB) for growth of *Shigella*. LIA slants were inoculated and read as before. Presumptive *Salmonella* and *Shigella* growths on LIA were streaked to obtain pure cultures. An oxidase test utilizing dimethyl-p-phenylenediamine hydrochloride was performed on these isolates (MacFaddin, 1976). Oxidase negative (absence of purple color) cultures were inoculated into Enterotubes (Roche Diagnostics, Nutley, NJ), a multi-media, rapid identification system. Reactions were recorded, and the presence or absence of *Salmonella* and *Shigella* was ascertained.

RESULTS AND DISCUSSION

Freshly harvested, properly stored shellfish destined to be marketed in North Carolina usually may be expected to have standard plate counts less than 10,000 SPC/g (George Gilbert, 1978). SPC's higher than this were recorded in *Rangia* throughout the study period (Table 1), confirming findings of the state shellfish sanitation authorities. Log means of the counts ranged from 31,000 SPC/g (October) to 4,900,000 SPC/g (December). There was no statistical correlation between these total counts and month or water temperature. There was, however, an association between the SPC and site (station number) over the entire twelve month study. The SPC's were higher from stations with fresher water, reaching a log mean of 640,000 SPC/g at Station 4 in water closed to shellfishing (Table 1).

Bacterial spoilage of shellfish is caused by an exponential rate of increase of bacteria per gram of meat. Therefore, the onset of spoilage may be detected by analyzing the meats for the number of bacteria that grow aerobically on Standard Methods Agar (APHA, 1975). Shellfish that are improperly handled, processed, or refrigerated or products near the end of their shelf life will generally show an increase in SPC over freshly

TABLE 1. SPC-CLAMS

Month	Site	SPC/g	log	log mean (x)	10^x
JULY	1	100,000	5.000	4.746	56,000
	2	20,000	4.301		
	3	32,000	4.505		
	4	150,000	5.176		
AUG				4.798	63,000
SEPT				5.144	140,000
OCT				4.494	31,000
NOV				4.859	72,000
DEC				6.691	4,900,000
JAN				4.472	30,000
MAR				5.280	190,000
APR				5.470	300,000
MAY				5.688	470,000
JUNE				5.186	150,000

Site	log mean (x)	10^x
1	4.771	59,000
2	4.818	66,000
3	5.064	120,000
4	5.809	640,000

harvested shellfish. Sanitation authorities at some markets use 500,000 SPC/g as an indicator of product spoilage by bacteria.

Clams taken during our investigation sometimes showed counts near or occasionally exceeding this number. However, these were fresh clams harvested, iced immediately, and analyzed within 24 h of collection. These relatively high total bacterial counts then are not evidence of product spoilage, but rather indicate a naturally high bacterial flora in this clam. In addition, there was no statistical correlation between clam SPC's and the number of indicator organisms or potential pathogens.

The National Shellfish Sanitation Program has established a fecal coliform MPN limit of 230 FC/100g for shucked oysters. This standard does not specifically apply to all shellfish. Our twelve month collection of 48 clam samples had a median MPN of only 80 FC/100 g, but 11 of 48 or 23% of the samples exceeded 230 FC/100 g (Figure 4). A closer look at these counts provides interesting observations.

First, the highest FC values were recorded at Station 1, with a median MPN of 220 FC/100 g and 33% of the collections exceeding 330 FC/100 g. This finding is somewhat in conflict with expected results of lower FC values at higher salinities (Ketchum et al., 1952; Carlucci and Pramer, 1960) and longer exposure in both time and distance from sources of river discharge farther up the sound (Kittrell and Furfari, 1963; Lin et al., 1974).

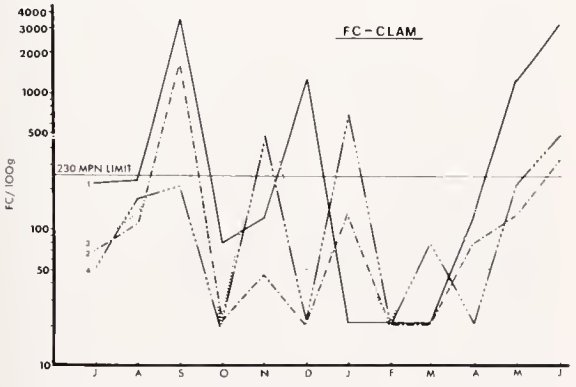

FIGURE 4. *Fecal coliform counts in clams, July 1977 to June 1978. Numbered lines indicate the four sampling stations.*

There are two factors that may have contributed to those higher FC densities. The water at this collection point is isolated from easy mixing with the rest of Roanoke Sound by a spit of sand about 50 m offshore running parallel to the shore for at least 100 m. Thus, there is a lagoon formed which could provide containment of surface water runoff. There are also a number of homes along the shore utilizing septic tanks. While there is a chance that one of these systems could be malfunctioning and adding coliforms to the lagoon, the shellfish sanitation officer responsible for shoreline surveys indicated that the location of the tanks and disposal fields make this possibility for contamination remote.

Second, *Rangia* clams met the FC standard for a three month period of the study. From February through April, 1978, the median MPN for the 12 samples was 53 FC/100 g, with no samples exceeding 230 FC/100 g. It is impossible to state that this is a seasonal pattern of counts occurring annually that might allow for harvesting during these months. The possibility exists, but there are no continuous data from previous years. The counts may be highly variable, changing weekly or even daily. More frequent sampling over a longer period would provide an answer.

The numbers of potential pathogens detected were quite low. Vibrios, both NAGV and VPLO, were the most prevalent (Figure 5), following a characteristic pattern of greater numbers in water during the summer and lower values during winter months (Baross and Liston, 1970; Kaneko and Colwell, 1973). Vibrios are normal inhabitants of estuaries and estuarine biota. *Vibrio parahaemolyticus* is the major cause of food poisoning outbreaks in Japan, where much of the seafood is eaten raw. The incidence of vibrio-related gastroenteritis is much lower in the United States, but *V. parahaemolyticus* is still the major etiologic agent in outbreaks caused by consumption of seafood in this country (Center for Disease Control, 1971-1976). However, none of these outbreaks have been attributed to consumption of raw products, such as oysters and clams. Sufficient cooking temperature, elimination of cross contamination, and adequate refrigeration should prevent any health hazards posed by this bacterium.

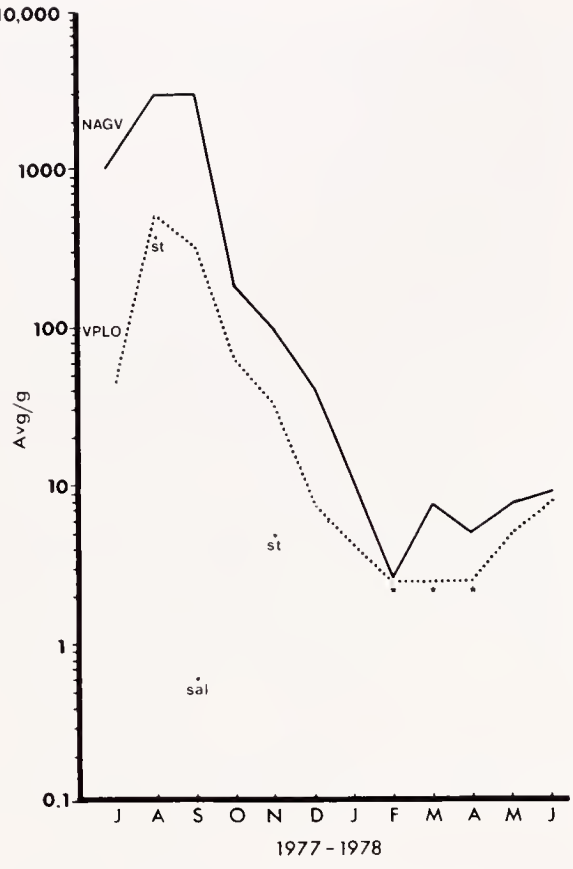

FIGURE 5. *Potential pathogen counts in clams, July 1977 to June 1978. Starred points indicate actual* Vibrio *values of <2.5/g. Such values were not plotted for* Staphylococcus.

Coagulase positive staphylococci (st), those staphylococci most commonly causing illness in man, were found in 5 of 40 clam samples. Four of these samples were from the August, 1977, collection in which clams from each of the 4 stations contained this bacterium. The average number detected that month for the 4 sample sites was 380 st/g (Figure 5). This value included those isolates found to be weakly coagulase positive. Most estimates indicate that it takes at least one million staphylococci to produce enough enterotoxin to cause intestinal disorder in humans (Jay, 1978).

Cultures presumptively identified as salmonellae (sal) were reported on only one sample date. The MPN procedure used at that time in the study yielded a count of 0.6 sal/g (Figure 5). This quantity of salmonellae, even if confirmed, is very low in regard to minimum infective dose for these organisms. In most cases of salmonellosis, millions of bacteria must be ingested (Bryan, 1975).

In February 1978, 8 isolates produced reactions on LIA slants presumptive for *Shigella*. Because this bacterium had not been detected before this time, the cultures were subjected to further diagnostic procedures (Figure 3). All of the 8 presumptive shigellae were found to be false positive.

Shelf life studies, designed to determine the best methods of storage, were conducted. Dry refrigerated shellstock (4°C) showed no significant increases in SPC at 5 days and exhibited only a threefold increase in 12 days. Fresh clams that were shucked and stored at the same temperature did not store as well showing a threefold increase in SPC in 5 days and a twentyfold increase in 12 days.

Our data confirmed the presence of high SPC's as reported by state shellfish sanitation authorities. However, the SPC, in itself, is of minor sanitary significance in freshly harvested shellfish without comparison to fecal coliform or potential pathogen counts. No correlation was observed between clam SPC's and the levels of fecal coliforms or potential pathogens monitored in this study. Fecal coliform standards for oysters were exceeded by a fraction of the clam samples, but more data are needed from approved water areas before a judgment can be made concerning compliance with this standard. The low recovery of potential pathogens is significant in regard to sanitary quality and proposed marketability. It cannot be stated that the bacterial flora of *Rangia* presents no threat to public health. Potential health hazards exist in the consumption of any shellfish, raw or processed. Our findings of approximate compliance with fecal coliform standards and low numbers of potential pathogens indicate that *Rangia* when harvested from approved waters, poses no unique public health risk.

The resource potential of *Rangia* based on sheer abundance in North Carolina's estuaries and interest by fishermen seems promising. Other studies recognize the very real market potential of *Rangia* (Hopkins et al., 1973; Chestnut and Porter, 1976). No evidence presented in this report

supports arguments against marketing this clam as a cooked product. Fresh marketing apparently may require special handling, special limits as to water conditions or season, and waiver of the SPC as a market criterion.

ACKNOWLEDGEMENTS

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LITERATURE CITED

American Public Health Association. 1970. Recommended procedures for the examination of seawater and shellfish. 4th ed. APHA, Washington, D.C.

American Public Health Association. 1975. Standard methods for the examination of water and wastewater. 14th ed. APHA, Washington, D.C.

Anonymous. 1964. Little-neck clams appear promising. N.C. Commercial Fisheries Newsletter. 1:1-2.

Baross, J. and J. Liston. 1970. Occurrence of *Vibrio parahaemolyticus* and other hemolytic vibrios in the marine environment of Washington State. Appl. Microbiol. 20:179-186.

Bowden, W. B. and J. E. Hobbie. 1977. Nutrients in Albemarle Sound, North Carolina. Univ. of North Carolina Sea Grant College Publ. UNC-SG-75-25.

Bryan, F. L. 1975. Status of foodborne disease in the United States. J. Environ. Health. 38:74-83.

Cain, T. D. 1975. Reproduction and recruitment of the brackish water clam *Rangia cuneata* in the James River, Virginia. Fish. Bull. 73:412-430.

Carlucci, A. F. and D. Pramer. 1960. An evaluation of factors affecting the survival of *Escherichia coli* in seawater. II. Salinity, pH, and nutrients. Appl. Microbiol. 8:247-250.

Center for Disease Control. Foodborne and Waterborne Disease Outbreaks, Annual Summaries 1971-1976. Issued 1972-1977.

Chestnut, A. F. and H. J. Porter. 1976. Comprehensive report on the brackish water clam, *Rangia cuneata* (Gray), industry in North Carolina. Unpublished manuscript. College of Marine Studies. Univ. of Delaware. pp. 1-10.

Darnell, R. M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci., Univ. of Texas. 5:353-416.

Food and Drug Administration. 1976. Bacteriological analytical manual. 5th ed. U.S. Dept. H.E.W., Washington, D.C.

Gilbert, G. 1978. Personal communication. Shellfish Sanitation Program, N.C. Dept. Human Resources, Morehead City, N.C.

Godwin, W. F. 1968. The distribution and density of the brackish water clam, *Rangia cuneata*, in the Altamaha River, Georgia. Georgia Game and Fish Comm., Mar. Fish. Div., Contr. Ser. 5, pp. 1-10.

Hoese, H. D. 1972. Abundance of the low salinity clam, *Rangia cuneata*, in southwestern Louisiana. Paper presented at the annual meeting of the National Shellfisheries Association, 1972.

Hopkins, S. H., J. W. Anderson, and K. Horvath. 1973. The brackish water clam *Rangia cuneata* as indicator of ecological effects of salinity changes in coastal waters. Report to U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Miss. Contr. Rep. H-73-1.

Hopkins, S. H. and J. D. Andrews. 1970. *Rangia cuneata* on the East Coast: Thousand mile range extension, or resurgence? Science. 167:868-869.

Jay, J. M. 1978. Modern food microbiology. D. Van Nostrand Co., New York, N. Y.

Kaneko, T. and R. R. Colwell. 1973. Ecology of *Vibrio parahaemolyticus* in Chesapeake Bay. J. Bacteriol. 113:24-32.

Ketchum, B. H., J. C. Ayers, and R. F. Vaccaro. 1952. Progress contributing to the decrease of coliform bacteria in a tidal estuary. Ecology. 33:247-248.

Kittrell, F. W. and S. A. Furfari. 1963. Observations of coliform bacteria in streams. J. Water Pollut. Control Fed. 35:1361-1385.

Lewis, K. H. and R. Angelotti. 1964. Examination

of foods for enteropathogenic and indicator bacteria. Pub. Health Serv. Publ. No. 1142. Supt. of Documents, U.S. Govt. Printing Office, Washington, D.C.

Lin, S., R. L. Evans, and D. B. Beuscher. 1974. Bacteriological assessment of Spoon River water quality. Appl. Microbiol. 28:288-297.

MacFaddin, J. F. 1976. Biochemical tests for identification of medical bacteria. The Williams & Wilkins Company, Baltimore, Md.

Pfitzenmeyer, H. T. and K. G. Drobeck. 1964. The occurrence of the brackish water clam, *Rangia cuneata*, in the Potomac River, Maryland. Chesapeake Sci. 5:209-212.

Singley, J. A. 1893. Contributions to the natural history of Texas. Part 1. Texas mollusca. Ann. Rep. Geol. Surv. Texas. 4(1892):297-343.

Speck, F. G. and R. W. Dexter. 1946. Molluscan food items of the Houma Indians. Nautilus. 60:34.

Suttkus, R. D., R. M. Darnell, and J. H. Darnell. 1954. Biological study of Lake Pontchartrain. Annual report 1953-1954. Zoology Dept., Tulane Univ.

Tenore, K. R., D. B. Horton, and T. W. Duke. 1968. Effects of bottom substrate on the brackish water bivalve, *Rangia cuneata*. Chesapeake Sci. 9:238-248.

Willis Brothers Seafood. 1978. Personal communication. Marshalburg, N.C.

INVITED PAPERS
1978 ANNUAL MEETING

The papers that appear in the following section were presented at the 70th Annual Meeting of the National Shellfisheries Association held in New Orleans, June 19-23, 1978. These papers represent a broad spectrum of ideas that the Program Committee felt should be made available to the membership. Each paper was invited and we are grateful to those who took the time and dedicated themselves in bringing these viewpoints to our attention. There were other invited papers presented that, because of time constraints and other mitigating factors, we were unable to have available in time for publication. The editors hope that these papers will be made available in future issues of the Proceedings.

Aaron Rosenfield
Program Chairman
National Marine Fisheries Service
Oxford, Maryland

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ULTRASTRUCTURAL MORPHOGENESIS OF PRODISSOCONCH AND EARLY DISSOCONCH VALVES OF THE OYSTER *CRASSOSTREA VIRGINICA*

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ABSTRACT

Results are reported on an investigation with the scanning electron microscope on the ultrastructure of valves of the American oyster, Crassostrea virginica *(Gmelin), emphasizing normal developmental ultramorphology of prodissoconchs I and II and newly set dissoconchs raised under favorable hatchery conditions. Developmental anatomical features described by early malacologists by light microscopy are reviewed, and structures visible only by scanning electron microscopy are described for the first time. Terms for larval stages are defined. Mineralogical determinations confirmed earlier reports that prodissoconch II valves of this species are aragonitic, and showed for the first time that valves of prodissoconch I are also aragonitic. Development of the following structures was examined: prodissoconch I and II valves, punctuate-stellate pattern on exterior of prodissoconch I valves, valve edges, prodissoconch I-II transitional band, provinculum, terminal and denticular hinge teeth, larval and spat ligament, resilium, fasciole and notch, prodissoconch II — dissoconch metamorphic juncture, adductor muscle scar, granular homogeneous shell, prismatic calcite of both dissoconch valves, and terraced and chalky foliated calcite. Transition from homogeneous aragonite of prodissoconch to foliated and prismatic structure of dissoconch is sharp. Larval teeth of prodissoconch II are obliterated by deposition of dissoconch shell, and the pivotal axis shifts anterior to larval umbones where a prominent inner ligament forms during prodissoconch stage and subsequently develops into ligamental resilium of spat.*

INTRODUCTION

Several investigators have described the shell of early stages of the American oyster, *Crassostrea virginica* (Gmelin), by light microscopy. This research is reviewed by Rees (1950), Carriker (1951), Stenzel (1971), and Dinamani (1976). With the exception of one micrograph by Dinamani (1976) of the hinge of a larva 250 μm long, there are no published reports on the ultrastructure of prodissoconch and early dissoconch valves of this species. Ultrastructural investigations of valves of early stages of other species of oysters are similarly limited (Dinamani, 1976). This is surprising in view of the economic importance of oysters and the proliferation of papers on the ultrastructure of valves of other molluscan larvae (see, for example, Robertson, 1971; Thiriot-Quievreaux, 1972; Giusti, 1973; Turner and Boyle, 1974; Richter and Thorson, 1975; Boyle and Turner, 1976; LePennec and Masson, 1976; Waller, 1976; and Togo, 1977).

The current emphasis on culture of commercial species of oysters in various types of controlled systems (Price et al., 1976), and the importance of information on normal shell ultramorphology as a basis for comparison with anatomical and functional anomalies which may occur in mariculture, prompted us to undertake the present study. There were also other considerations. For example, the shape, thickness, strength, coloration, and ornamentation of oyster dissoconch valves reflect environmental conditions (Galtsoff, 1964; Palmer and Carriker, 1979). Whether the ultrastructure of valves of prodissoconchs and early dissoconchs also reflects growing conditions has yet to be determined; the present study provides a background and stimulus for such investigations in the future. Furthermore, the remarkable capacity of bivalves to concentrate chemical elements in their soft and calcareous tissues is well documented (Galtsoff, 1964; Milliman, 1974; Frazier, 1975, 1976). Among others, factors involved in incorporation of chemical elements in shell include conditions of crystal growth, types of crystals, and differences in shell layers and other structures (Wilbur, 1972; 1976). It is clear that analysis of these factors also depends upon a knowledge of shell ultrastructure.

The present publication is the first reporting results of a comprehensive investigation with the scanning electron microscope (SEM) of the ultrastructure of the valves of *Crassostrea virginica* (Gmelin), and concentrates on the normal developmental ultramorphology of the valves of prodissoconchs I and II and newly set dissoconchs raised under favorable hatchery conditions. Developmental features described by early malacologists by light microscopy are reviewed and new structures not visible with the light microscope are described for the first time.

MATERIALS AND METHODS

Oysters.

Larvae and spat of *Crassostrea virginica* were raised in the maricultural facility of the College of Marine Studies, University of Delaware in Lewes, Delaware (Pruder et al., 1976). Brood stock were collected in the Broadkill River near Lewes, and conditioned and spawned (Maurer and Price, 1967) in the hatchery of the maricultural facility. Four different larval broods, from mixed parents, were reared in 400-ℓ conical tanks from November 1977 to June 1978. Water in the larval tanks was changed every second day with seawater of an approximate salinity of 30 $^{0}/_{00}$ collected at high tide at Indian River Inlet, Delaware. Temperature of the seawater in larval tanks ranged from 27 to 28°C. Larvae were fed an algal mixture of approximately 60% *Thalassiosira pseudonana* 3H Hasle et Heimdal and 40% *Isochrysis galbana* Parke at an initial concentration of roughly 50,000 cells ml^{-1}. Pediveligers were allowed to set on sheets of mylar film to facilitate study of the relationship of the attached left valve to the substratum.

Preparation of valves for scanning electron microscopy (SEM).

(a) Cleaning. Live prodissoconch I larvae were placed in 2% clorox (0.1% sodium hypochlorite; clorox = 5.25% sodium hypochlorite) alkalized with NaOH to a pH of approximately 10 (S.E. Siddall and R.A. Lutz, personal communication) and left in the solution for 10 min. During this time soft tissues were dissolved and valves were cleaned. However, about 30 min were required in the solution before the larval ligament dissolved sufficiently to allow valves to separate. Prodissoconch II and early dissoconch valves were more difficult to clean and separate and required immersion in a 5% alkalized solution of clorox (0.26% sodium hypochlorite) for 40 min to 2 hr. Sonication in the clorox solution and raising the temperature of the solution to about 60°C accelerated dissolution of soft tissues and the larval ligament, but also tended to erode the valves. Larvae and spat were flushed onto a fine stainless steel screen which was dipped directly into solutions. The screen, immersed in a finger bowl of sodium hypochlorite solution, was placed under a binocular microscope, where progress of digestion of soft tissues and separation of valves was followed. Freezing live larvae and spat in seawater for several days not only maintained the valves in good condition for later study, but also killed the larvae in a gaping condition which hastened digestion of soft tissues by sodium hypochlorite. After cleaning, frozen larvae gaped more widely than those not frozen.

For study of the larval ligament, larvae which

had been frozen in seawater were left in fresh seawater at room temperature to allow microbiological activity to clean out soft tissues. This procedure removed soft tissues, but did not appreciably injure the hinge and ligament. Loose mucoid films from the valves were removed by dipping the valves in 2% clorox for about 15 sec and then rinsing them thoroughly in tap water (weakly acidic).

After rinsing, valves were pipetted into small concave dishes, excess water was drawn off, and the dishes were placed in an oven at 60°C to dry for several days. Valves were subsequently stored in vacuum desiccators in the small dishes.

Initial optical search for the ligament of pediveligers was done by staining valves, which had been cleaned microbiologically, with full strength Magalhaes' (1948) stain (equal parts 1% aqueous crystal violet and 0.3% aqueous basic fuchsin) for about 15 min. The ligament stained intensely, whereas valves themselves took up the stain only slightly. Intact gaping valves of the microbiologically cleaned pediveligers were then rinsed and dried for mounting.

(b) Mounting on SEM stubs. SEM aluminum pin stubs were cleaned in acetone, and valves of early stage larvae were placed directly on the surface of the stub in a drop of tap water. Excess water was blotted off with absorbent paper, and residual water was evaporated under the lamp of the microscope. The stub preparation was then thoroughly dried in an oven at 60°C for at least a day.

Late stage larval valves, dried in an oven, were scattered onto the surface of a 1:1 mixture of silver paint and clear fingernail polish applied to a SEM stub. The paint-polish mixture was slightly tacky but not soft enough to let the valves sink into the conductive adhesive. Progress of hardening of the mixture was followed under the binocular microscope by touching the surface with the tip of a fine needle. Nail polish reduced the tendency of the silver paint to flow onto the surface of specimens and did not contaminate the SEM column.

For the study of the ligament, larvae were mounted on double adhesive tape on aluminum pin stubs.

Small pieces of mylar film containing cleaned attached spat were cut from the setting sheet and glued to stubs with silver paint. Paint was also applied to the mylar film around each spat to reduce charging. Some right valves were separated from attached left valves and mounted exterior side down.

Mounting oyster valves on double adhesive tape was considerably easier than on the paint-polish mixture, but unfortunately the tape tends to contaminate the SEM column and impairs resolution so it was used only when other mounting media were unsuitable.

Fractured sections of larval valves were prepared in two ways. In the first, valves were crushed slightly between a microscope slide and cover slip and then the valve fragments were scattered onto the hardening surface of silver paint-nail polish. In the second method, a fragment of cover slip was pressed gently onto the surface of a stub on which valves had been mounted until the desired amount of breakage had been achieved.

Before examination in the SEM, specimens and stubs wers coated in vacuum with two or more coats of carbon and gold (400-600A). Heavy coats were necessary to reduce charging, especially with prodissoconch I valves, which appear to contain a high proportion of organic material.

(c) Identification of crystal type. Cleaned valves of prodissoconch I and II were analyzed by X-ray diffraction by mounting entire valves on the revolving spindle of a Gandolfi camera, or by staining valves with Feigel's solution (Milliman, 1974). Aragonite turns black in the solution, and calcite remains colorless.

ULTRASTRUCTURE AND MINERALOGY OF VALVES OF LARVAL AND EARLY DISSOCONCH STAGES

Dimensions and Terminology.

Sibling oyster larvae maintained under identical conditions of culture grow at widely different rates and matamorphose at different times (Loosanoff and Davis, 1963; Newkirk et al., 1977; observations in maricultural facility, College of Marine Studies). For this reason, in the following account we will identify larval stages primarily by form and size rather than by age. At normal summer temperatures in the mid-Atlantic area oyster larvae generally start setting about two weeks

after fertilization, although specific rate of development may vary with temperature.

Considerable variation has been reported on the maximal larval size of *Crassostrea virginica* along the Atlantic seaboard, there being a tendency for larvae to set at a larger size in northern than southern latitudes. A range of maximal length of 248 to 400 μm has been recorded by various investigators (Carriker, 1951).

Dimensions of larval valves of *Crassostrea virginica* during development from the first shelled stage to setting have been recorded by Chanley and Andrews (1971) for larvae from Virginian estuaries as follows: length, 60 to 350 μm; height, initially 10 μm less than length, increasing to equal length at 90-100 μm, and eventually exceeding length by as much as 15 μm; width, 35 to 40 μm less than length, increasing to 100 μm less than length in late stages; hinge line, 45 to 50μm long. Metamorphosis occurs at a length ranging from 310 to 350 μm. Valves are round at a length of 80 to 100 μm, and become knobby at 85 to 125 μm (see also careful work of Loosanoff and Davis, 1963; Galtsoff, 1964; Forbes, 1967).

Some confusion exists on terms used for larval stages of bivalves (Carriker, 1961; Chanley and Andrews, 1971; Stenzel, 1971; and others). Because of this we describe briefly terms employed in this paper with reference to those used by other investigators.

Dimensions of height, length, and width of shelled larvae are defined as follows (Galtsoff, 1964): *height*, distance between umbo and ventrum; *length*, anteroposterior distance; *width*, maximal distance between exterior surfaces of the right and left valves (Chanley and Andrews, 1971, used the term depth for width).

Prodissoconch I. First shelled stage developing from nonshelled veliger. It bears thin, uniform, smooth, transparent valves secreted by the shell gland and mantle epithelium (Kume and Dan, 1968). The D-shaped or straight-hinged veliger refers to the shape at both prodissoconch I and early prodissoconch II valves. Stenzel (1971) refers to prodissoconch I as the phylembryo or protostracum veliger.

Prodissoconch II. New shell is added by the mantle both around the edges of and inside prodissoconch I valves. The new shell bears concentric growth striae which clearly distinguish it from shell of prodissoconch I. From a round shape, the valves soon become umboned and asymmetrical, the left larger than the right, and the anterior end of the valves becomes more pointed than the posterior end. The umbones point posteriorly. Stenzel (1971) refers to this stage as the prodissoconch veliger, and omits the terms prodissoconch I and II.

Pediveliger. This is the prodissoconch II stage in which velum, foot, and eyes are fully developed, and the bivalve is preparing to set.

Dissoconch. As soon as settlement and matamorphosis occur, the mantle of the spat (juvenile oyster) initiates secretion of the adult form of shell structure. A sharp transitional line of demarcation, the *metamorphic line*, is clearly evident at the boundary between prodissoconch II and the early dissoconch.

Confusion also exists on the terminology for regions and ultrastructural units of the shell of oysters and other bivalves (Tsujii et al., 1958; Watabe et al., 1958; Watabe and Wilbur, 1961; Wada, 1963; Watabe, 1965; Taylor et al., 1969; Kobayashi, 1971; Waller, 1975; Wilbur, 1976). We have adopted the terminology proposed by Taylor et al. (1969) for *Crassostrea virginica* as follows:

The exterior of dissoconch valves is covered by a very thin organic *periostracum*. This lies over the thin layer of *prismatic calcite* visible externally near valve margins (primarily of the right valve) as overlapping layers of *imbricated scales* ("spurs" of Nakahara and Bevelander, 1971). On older portions of valves the prismatic structure is generally worn off. Prismatic calcite is composed of individual *prisms*, each a mineral core within an organic envelope. The bulk of the valves is composed of *foliated calcite* (the calcitostracum, subnacreous, or nacreous layer of several authors). This region consists of fine sheets, or *folia* (or laminae), grouped into larger *lenticular folia*. Individual folia are composed of small elongate *laths* (the tablets or lamellae of other authors), joined together by organic matrix, and on the interior surface of valves frequently resemble tiles on a roof. Lenses of *chalky shell*, consisting of laths ar-

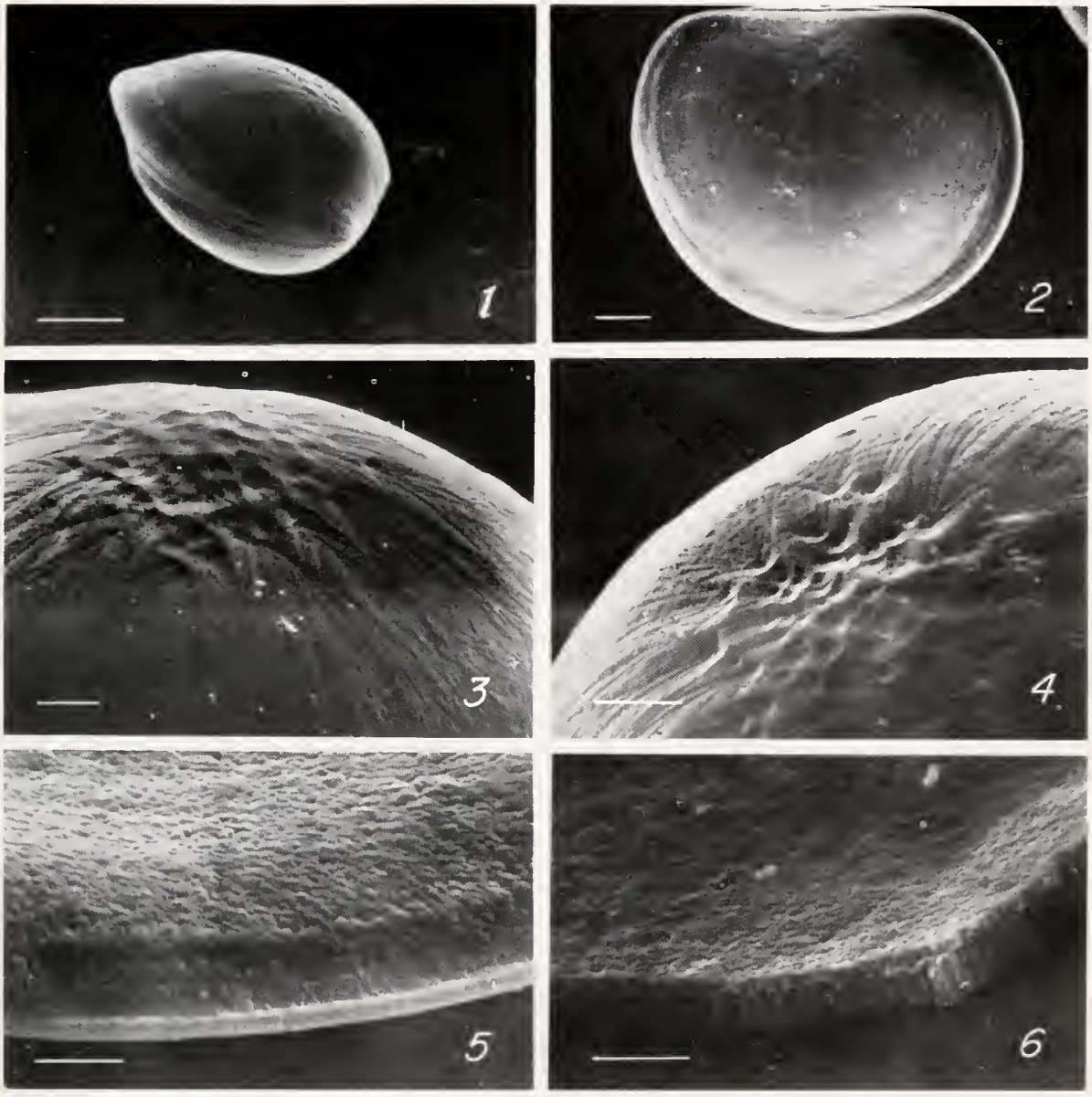


FIGURE 1. *Prodissoconch I, ventrolateral view. Rim of prodissoconch II forming. 2% clorox 6 min. Scale bar = 20 μm.*

FIGURE 2. *Prodissoconch I. Valve view. Narrow rim of prodissoconch II shell forming. Treated in 2% clorox for 10 min. Scale bar = 10 μm.*

FIGURE 3. *Prodissoconch I. Punctate-stellate pattern on one valve. 2% clorox 75 min. Scale bar = 5 μm.*

FIGURE 4. *Prodissoconch I. Punctate-stellate pattern on one valve, higher magnification than Figure 3. 5% clorox 23 min, and 3 min sonication. Scale bar = 5 μm.*

FIGURE 5. *Prodissoconch I-II. Interior view of edge of valve showing thin outer layer (0.5 μm thick) of prodissoconch I valve; inner surface of granular shell units of prodissoconch II valve. 2% clorox 10 min. Scale bar = 2 μm.*

FIGURE 6. *Prodissoconch I-II. Fractured section of valve and interior of valve. Fracture 1 μm thick. Scale bar = 2 μm.*

ranged irregularly in a spongy pattern, occur frequently in foliated structure.

Mineralogy.
Mineralogical determinations confirmed Stenzel's (1964) report that prodissoconch II valves of larvae of *Crassostrea virginica* are aragonitic, and demonstrated for the first time that valves of prodissoconch I are also aragonitic.

Prodissoconch I.
The D-shaped, straight-hinged outline of prodissoconch I valves of *Crassostrea virginica*, when seen in side view by scanning electron microscopy (Figure 2), resembles the optical illustrations of this stage prepared by several investigators (Carriker, 1951). Not so evident in optical illustrations, however, is the considerable width of larvae even at this early stage. Rather than a thin, flattened wafer, the closed valves resemble an oblong, flattened globe (Figure 1).

Shortly after prodissoconch I valves are formed, mantle edges and mantle surfaces begin secretion of prodissoconch II. Along the margin of the valves the new shell takes the form at first of a narrow, transitional band, easily distinguished from prodissoconch I shell by its smooth exterior surface (Figures 1 and 2). This is followed by shell which is thicker and begins to show fine concentric growth striae (Figure 1).

Most conspicuous, however, and not described before in oysters, is the striking punctate-stellate pattern on the surface of the center of each prodissoconch I valve (Figure 1-4). The center of the pattern consists of shallow punctate marks ranging in diameter from about 0.5 to 3 μm (Fig. 3, 4). These merge peripherally with acutely pointed triangles which radiate and overlap over most of each valve. Concentric striae, about 0.3 μm apart, blend with the radial lines from the apexes of the triangles (Figure 4). The punctate portion of the pattern probably overlies the embryonic shell gland and represents initial mineralization of conchiolin (Trueman, 1951; Kume and Dan, 1968). The radiating triangles probably reflect activity of that part of the shell-secreting mantle epithelium peripheral to the shell gland.

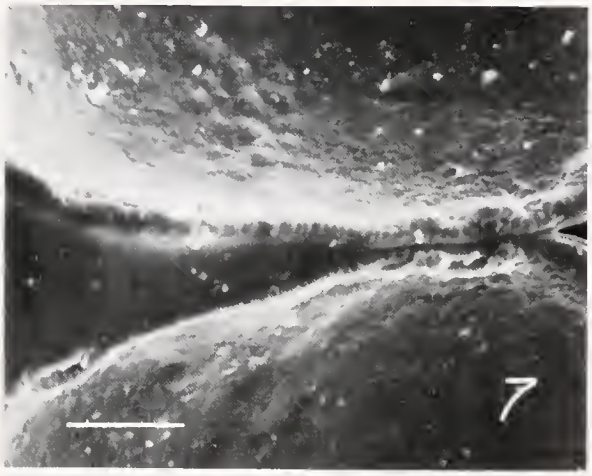
The edge of the valve of a larva 16 hours old seen from the interior shows a distinct outer layer about 0.5 μm thick (Figure 5). Inside this the shell consists of granular shell units ranging in diameter from 0.1 to 0.5 μm in surface view. A fractured section of a valve of a larva 19 hours old (Figure 6) is about 1 μm thick and is composed of an exterior layer approximately 0.7 μm thick (probably prodissoconch I) and an inner layer (probably prodissoconch II) of granular shell units, about 0.3 μm thick, probably partly exposed by action of the clorox. Granular units in the fractured section range in diameter from about 0.05 to 0.1 μm.

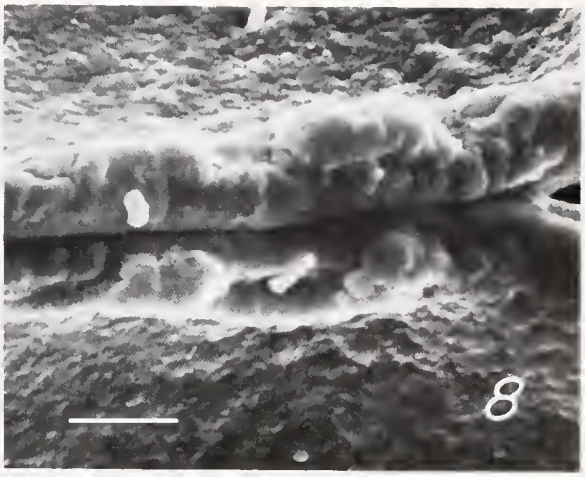
As valves of prodissoconch I grow, the provinculum (the primitive hinge apparatus, Rees, 1950; Galtsoff, 1964) thickens, and rudimentary swellings on the anterior and posterior ends develop into small, well-defined interlocking provincular teeth (Figures 7-10). By very early prodissoconch II stages, these have developed into one large taxodont tooth on each end of the provinculum of one valve, and two large taxodont teeth on each end of the other valve, with corresponding interlocking sockets in opposing valves (Figure 10). Length of the provinculum is about 45 μm (Figures 7 and 9). The space between the large side teeth is at first covered with shallow corrugations (Figures 7 and 9); these soon develop into minute denticles. Dentition is thus essentially heterodont (Dinamani, 1976). Length of each side tooth ranges from 4 to 5 μm. The granular nature of the shell units in the valves, and especially around the provinculum, is clearly shown in Figure 10. Largest granules measure about 0.4 μm.

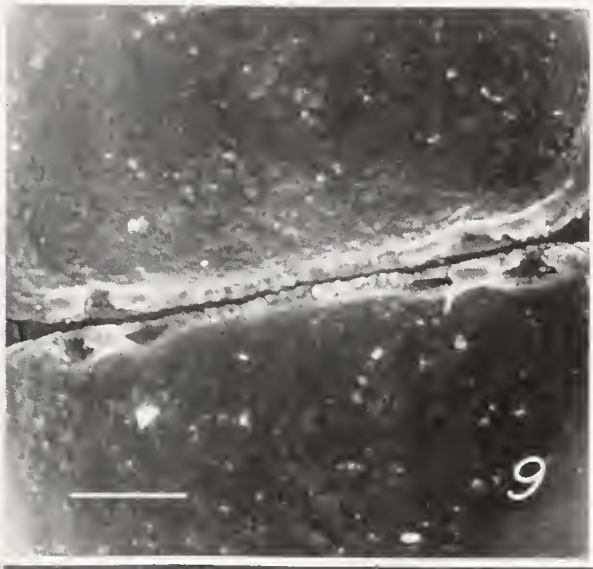
Prodissoconch II.

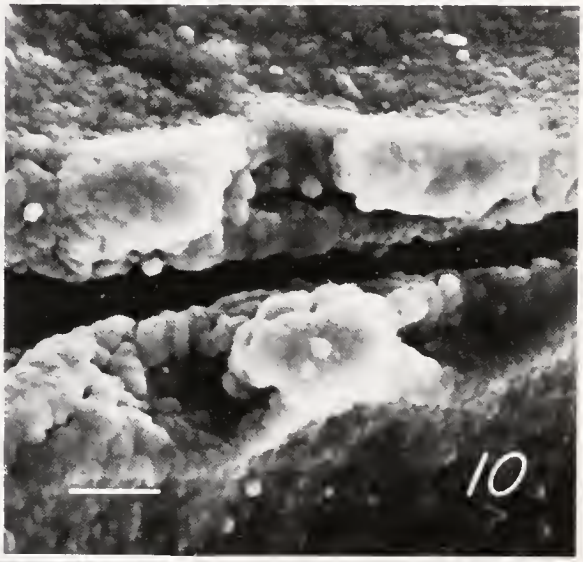
As larvae increase in size, their valves become unequal, the left valve (the future attached valve of the spat) growing considerably wider than the right, and the left umbo projecting farther from the provinculum than the right one (Figures 14 and 17). Umbones grow and point posteriorly as valves develop (Figures 16 and 17). The prodissoconch I-II transitional band becomes conspicuous, particularly in side view (Figures 14 and 15) and ranges in width from about 7 to 8 μm. The punctate-stellate pattern on the exterior surface of the valves of prodissoconch I persists through prodissoconch II (Figure 13).

As development proceeds, umbones come close together medially (Figure 17), preventing valves from opening widely. A laterodorsoanterior view









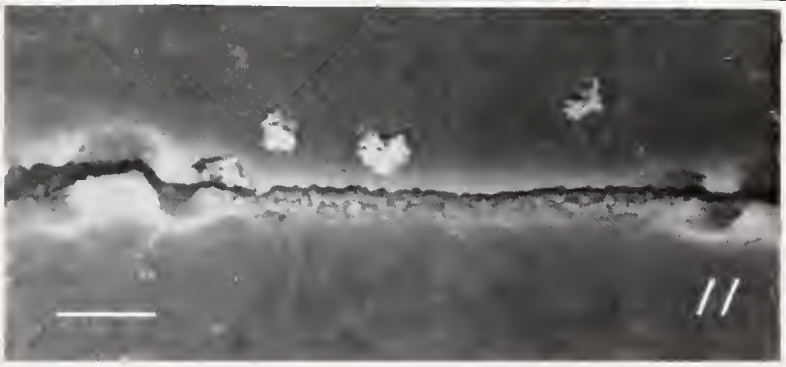


FIGURE 7. *Prodissoconch II. Provinculum, 45 μm long, of matching pair of valves. Taxodont terminal teeth forming at right end. 2% clorox 10 min. Scale bar = 10 μm.*

FIGURE 8. *Higher magnification of terminal teeth in provinculum of valves in Figure 7. Tooth on upper valve fits in socket of lower valve. Scale bar = 3 μm.*

FIGURE 9. *Prodissoconch II. Provinculum slightly more developed than that in Figures 7 and 8. Denticles starting to form between terminal teeth. 2% clorox 10 min. Scale bar = 10 μm.*

FIGURE 10. *Large terminal teeth of left end of provinculum shown in Figure 9. Scale bar = 2 μm.*

FIGURE 11. *Prodissoconch II. Provinculum. Cleaned microbiologically. No larval ligament evident. Scale bar = 5 μm.*

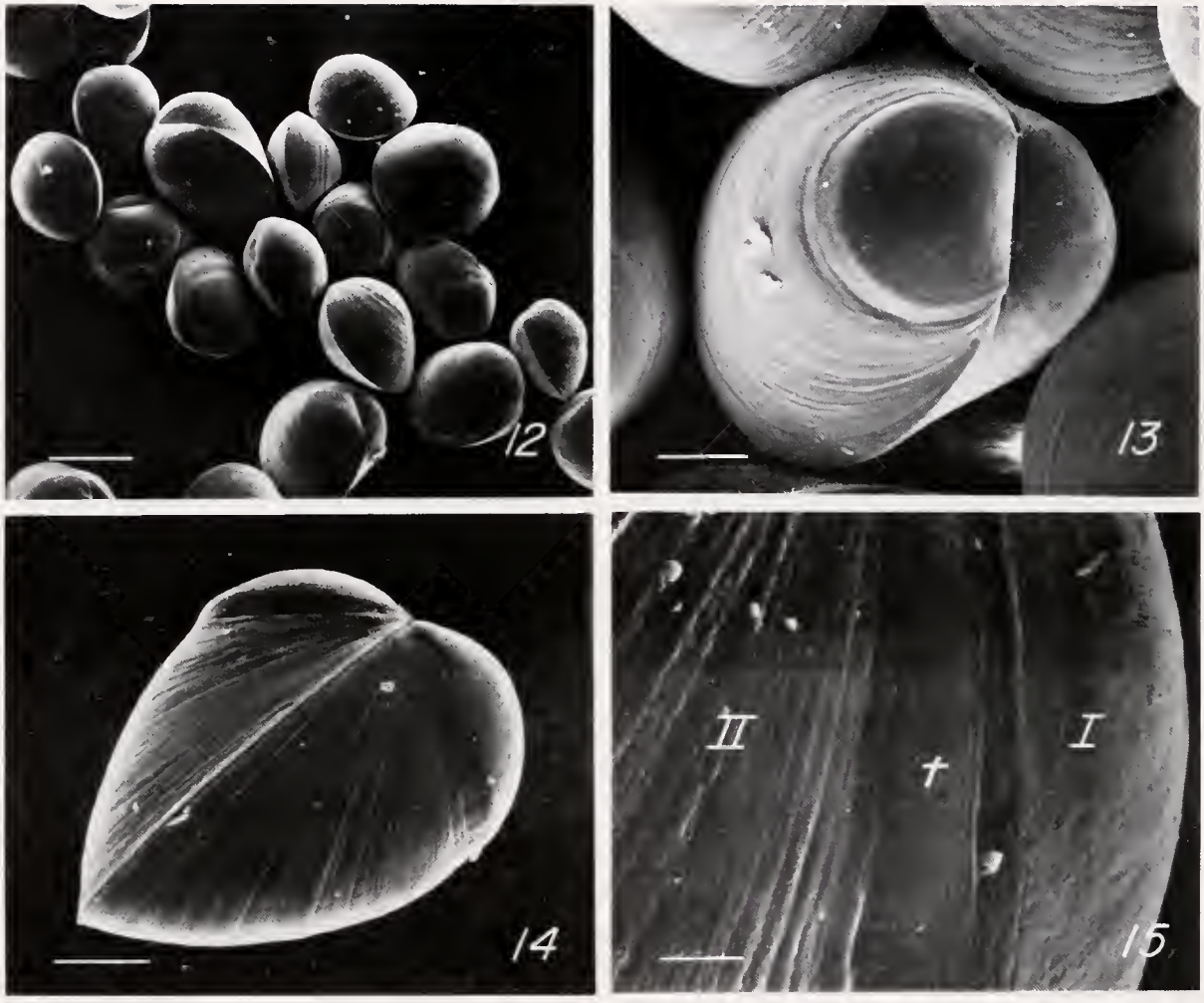


FIGURE 12. *Prodissoconch II. Larva to left of center has notch in right valve caused by injury during culture. 5% clorox 10 min. Scale bar = 100 μm.*

FIGURE 13. *Prodissoconch II. Umbonal (dorsal) view of larval valves, and punctate-stellate pattern of Prodissoconch I. 5% clorox 10 min. Scale bar = 20 μm.*

FIGURE 14. *Prodissoconch II. Side view of larval valves. 5% clorox 23 min, 3 min sonication. Scale bar = 20 μm.*

FIGURE 15. *Higher magnification of Figure 14 showing transitional band (t) between prodissoconch I (I) and II (II). Scale bar = 4 μm.*

of the valves (Figure 16) shows the marked flaring of the anterior and posterior sides that occurs with growth.

Prominent features of cloroxed exterior surfaces of prodissoconch II valves are close-set, conspicuous, concentric annulations (Figures 13, 14, 17, and 18). The finest of these growth striae are about 0.8 μm apart (Figure 18). Removal of the periostracum from the exterior surface with 5% clorox for 45 min exposed shell units on the exterior surface of the valves (Figure 19). The units are granular in nature and vary in size from 0.1 to 0.2 μm. Rod-like forms on the surface of the shell are probably remnants of periostracum left after treatment with clorox. At low magnifications, the interior of the valves appear smooth (Figure 21).

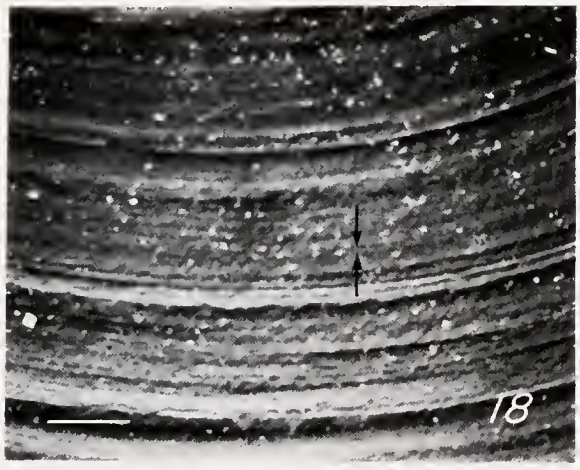


FIGURE 16. *Prodissoconch II. Laterodorsoanterior view of left valve of larva. 5% clorox 25 min, 6 min solication. Scale bar = 30 μm.*

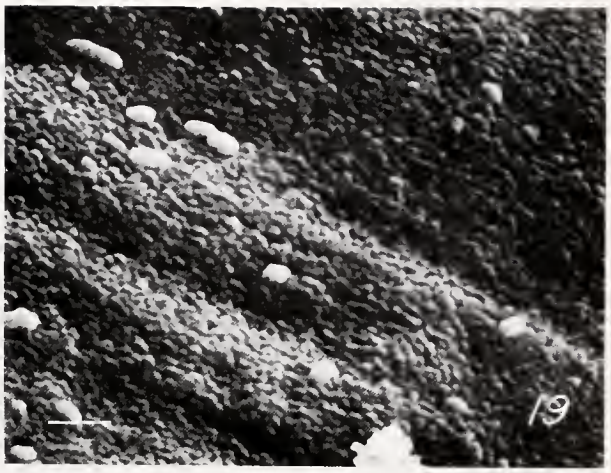


FIGURE 17. *Prodissoconch II. Umbonal view. 5% clorox 45 min. Scale bar = 30 μm.*

Contact of valve edges is tight when the shell is closed (Figures 12, 14, 16, and 20). As valves increase in size, rims in contact with each other become terraced internally (Figures 22 and 23), resulting in a step which runs around each valve up to the provinculum. The terracing is revealed by treatment of the shell with 5% clorox for about 45 min, which removes the periostracum. Shell units on the valve edge are granular and range in diameter from about 0.1 to 0.5 μm (Figure 23).

By the early prodissoconch II stage, the provinculum is well-developed (Figure 24); the terminal rectangular teeth, about equally developed on both sides of the provinculum, are large; and den-

FIGURE 18. *Prodissoconch II, pediveliger. Exterior surface of valve. Closest growth striae are 0.8 μm apart (see arrows). 5% clorox 45 min. Scale bar = 10 μm.*

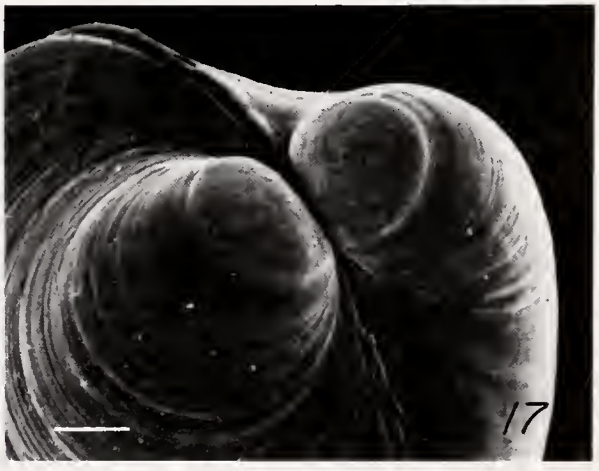


FIGURE 19. *High magnification of Figure 18 to show granular structure of exterior shell surface. Granules about 0.1 μm in diameter. 5% clorox 45 min. Scale bar = 1 μm.*

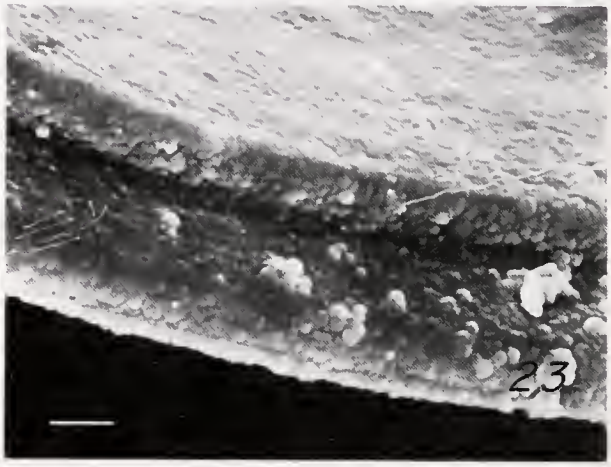


FIGURE 20. *Prodissoconch II. Ventral view of larval valves. 5% clorox 23 min, 3 min sonication. Scale bar = 20 μm.*

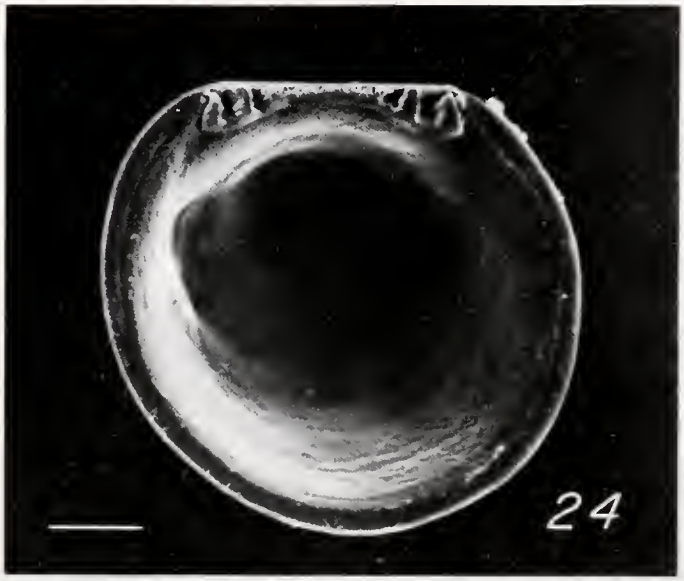
FIGURE 21. *Prodissoconch II, late pediveliger. Interior view of left valve. 5% clorox 45 min. Scale bar = 50 μm.*

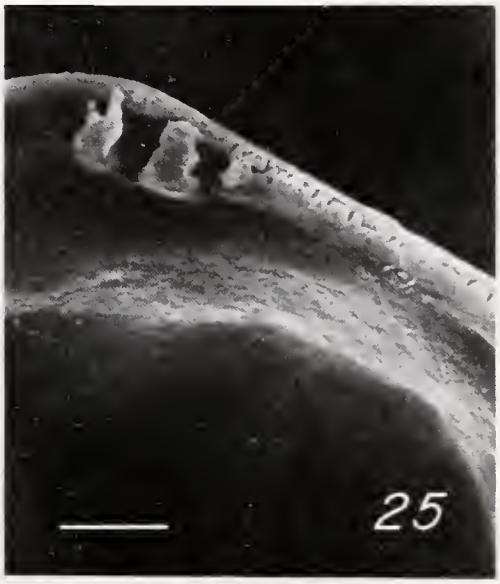
FIGURE 22. *Prodissoconch II, pediveliger. Side view of valves showing terraced edge exposed by immersion in 5% clorox for 45 min. Scale bar = 50 μm.*

FIGURE 23. *Prodissoconch II, pediveliger. Edge of valve to show terracing after treatment with 5% clorox for 40 min. Scale bar = 2 μm.*

ticles between them take the form of small rounded structures (Figures 25 and 26). As Dinamani (1976) also reported, terminal teeth are slanted toward the median at an acute angle. The length of the provinculum remains approximately the same as larvae grow; valve margins gradually encroach upon and outflank hinge ends (Stenzel, 1971). There are no flanges, or lateral or special teeth beyond the ends of the provinculum (Rees, 1950; Galtsoff, 1964), the terminal teeth serving to support the hinged valves. A view of the interior of the provinculum of intact valves shows how closely the teeth articulate (Figures 27 and 28).

By the mid-prodissoconch II stage, terminal teeth and intermediate denticles are well formed (Figures 29, 30, and 31). Two terminal teeth form at each end of the provinculum of the right valve (Figure 32), and three at each end of the provinculum of the left valve (Figures 29-31). Number and placement of teeth in *Crassostrea virginica* correspond to that in other species of larval oysters which have been examined (Imai, 1977).





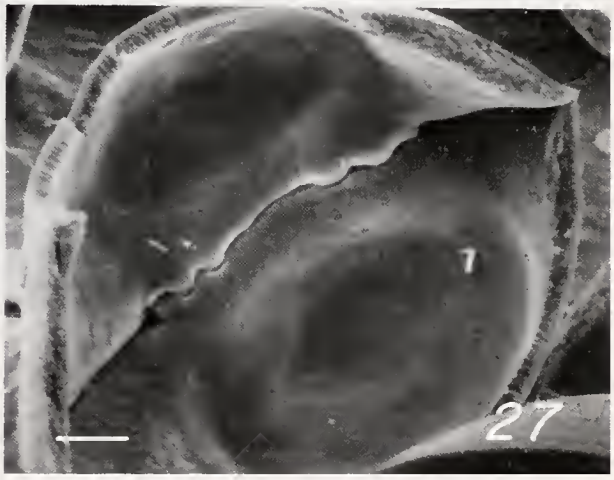


FIGURE 24. *Prodissoconch II. Left valve. 5% clorox 23 min. 3 min sonication. Scale bar = 20 μm.*

FIGURE 25. *Prodissoconch II. Left side of provinculum of left valve, similar to that in Figure 24. 2% clorox 20 min, 3 min. sonication. Scale bar = 8 μm.*

FIGURE 26. *Prodissoconch II. Provinculum of left valve. 5% clorox 40 min. Scale bar = 10 μm.*

FIGURE 27. *Prodissoconch II, middle stage. Interior of provinculum showing closeness of articulation of terminal teeth. 5% clorox 23 min, 3 min sonication. Scale bar = 10 μm.*

Terminal teeth bear conspicuous transverse grooves on their sides (Figures 30-32). These grooves and ridges minimize sheer on the hinge of shells which normally gape widely (Stanley, 1979; Waller, personal communication). By the early pediveliger stage, substantial amounts of shell have been added beyond ends of the provinculum (Figures 29 and 32) and a cardinal plateau, or ridge, about 20 μm wide, has been deposited between the terminal teeth on the right valve (Figure 32); this plateau interlaock with a socket between terminal teeth on the left valve (Figures 29 and 32).

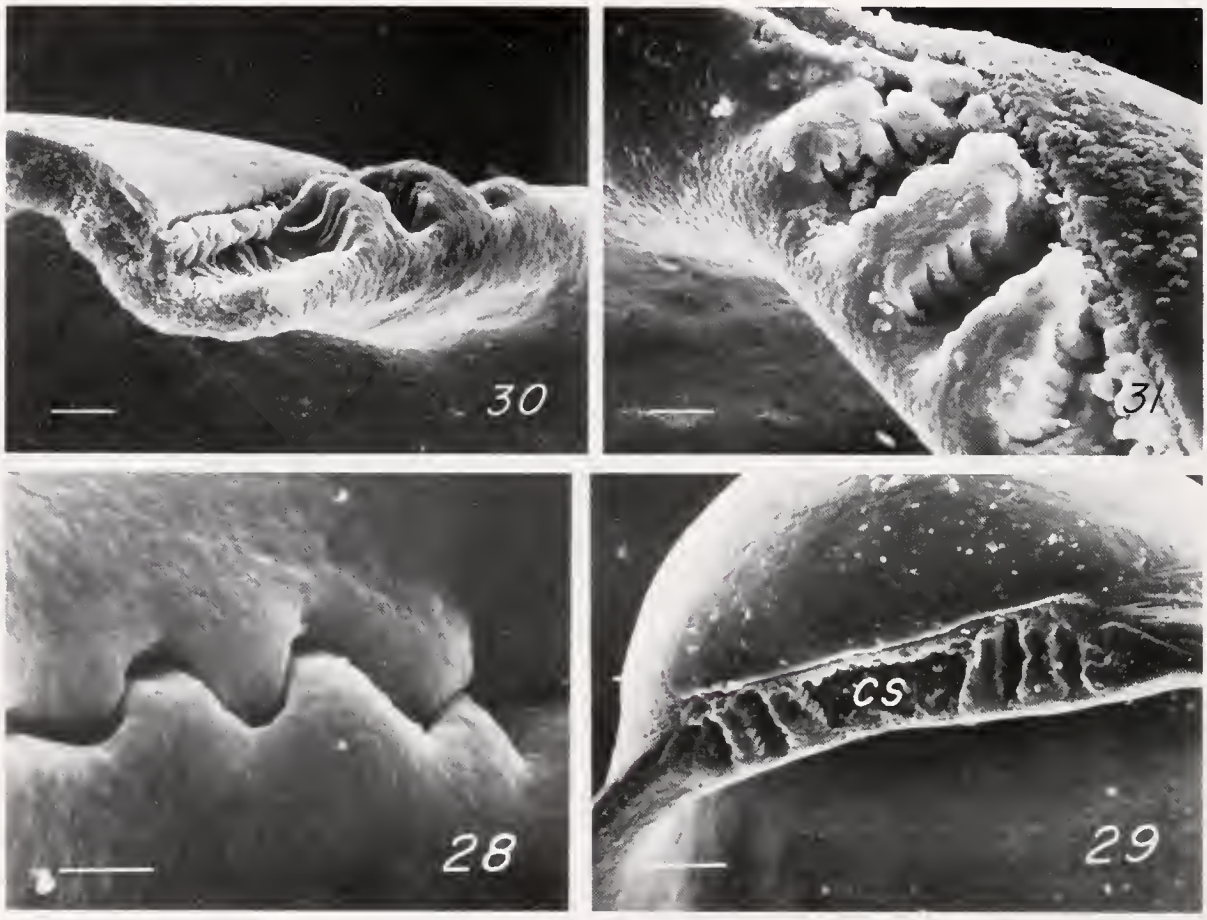


FIGURE 28. *Close view of terminal teeth in Figure 27. Scale bar = 3 μm.*

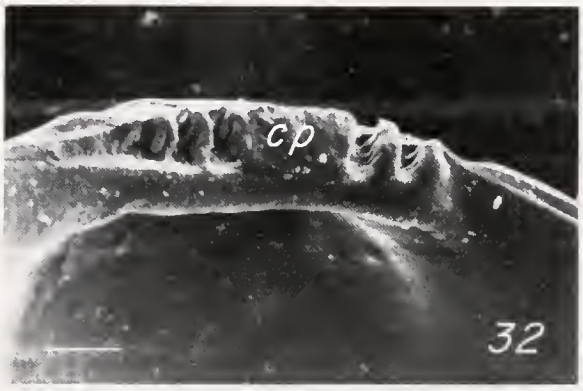
FIGURE 29. *Prodissoconch II, early pediveliger. Provinculum of left valve, showing cardinal socket (CS) between teeth ventral to denticles. 5% clorox 25 min, 6 min sonication. Scale bar = 10 μm.*

FIGURE 30. *Prodissoconch II, early pediveliger. Denticles and terminal teeth on anterior of provinculum of left valve. Hinge apparatus fractured in half after 5% clorox 25 min, and 6 min sonication. Scale bar = 5 μm.*

FIGURE 31. *Prodissoconch II, early pediveliger. Terminal teeth on posterior side of provinculum showing deep sockets between teeth and grooves on sides of teeth. 5% clorox 25 min, 6 min sonication. Scale bar = 3 μm.*

Denticles are still present, confined to the outer rim of the cardinal socket (Figure 33) and plateau. With continued growth, the provinculum of the late pediveliger begins to fill with shell, gradually obliterating the terminal teeth and denticles (Figure 33). By settlement, or early afterwards, the process of obliteration is completed. Deposition of shell begins at the posterior end of the provinculum and gradually advances anteriorly. The only published scanning electron micrograph of the larval shell of *Crassostrea virginica* is one of the provinculum of the left valve of a late prodissoconch II larva by Dinamani (1976, Figure 6a) which shows essentially what we have found. Pascual (1971) shows similar structures in light micrographs of the hinge of *C. angulata*.

The exterior of the larval hinge ligament is the thin nonmineralized layer laid down initially by



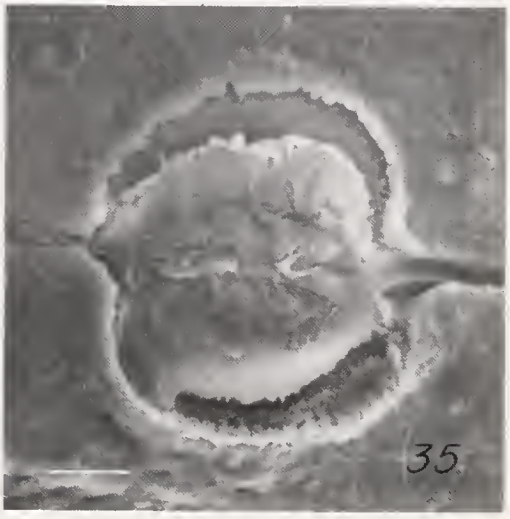


FIGURE 32. *Prodissoconch II, early pediveliger. Provinculum of right valve showing cardinal plateau (CP) between terminal teeth. Umbo is hidden behind hinge line. 5% clorox 40 min. Scale bar = 10 μm.*

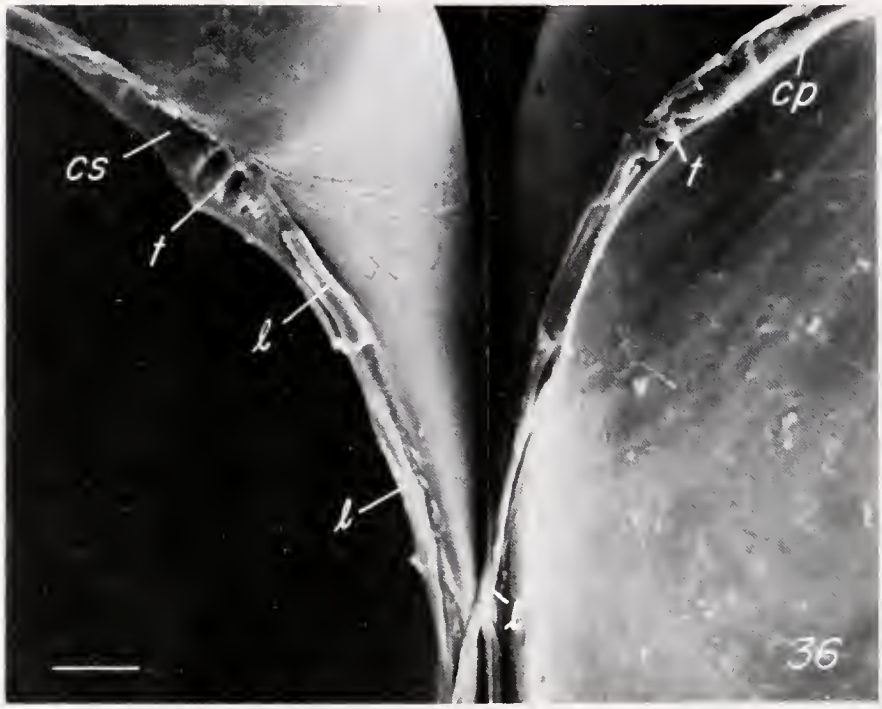
FIGURE 33. *Prodissoconch II, late pediveliger. Provinculum of left valve being obliterated by deposition of shell. 5% clorox 25 min, 6 min sonication. Scale bar = 10 μm.*

FIGURE 34. *Prodissoconch II, late pediveliger. Interior of provinculum in normally gaping valves to show inner larval ligament (l) and cardinal socket (CS). Cleaned microbiologically. Scale bar = 30 μm.*

FIGURE 35. *Prodissoconch II, inner larval ligament of late pediveliger in Figure 34, interior view. Scale bar = 5μm.*

the mantle epithelium. At first, valves are joined only by this membrane. The interior of the hinge of early prodissoconch II valves which were not treated with clorox show no evidence of an inner larval ligament (Figure 11).

At some stage of development of prodissoconch II (not determined precisely in this study) a small button-shaped inner larval ligament develops about 50 μm anterior to the anterior terminal teeth on the inside of the hinge. By the late pediveliger stage, the inner ligament, now about 20 μm in diameter, is a prominent feature of the inside of the hinge. The inner ligament was readily visible with the light microscope when stained with crystal violet and basic fuchsin after removal of soft tissues by microbiological activity. Scanning electron microscopy showed it even more clearly (Figures 34 and 35). The inner ligament appears to be continuous with the external ligament which has grown anteriorly to cover the dorsal



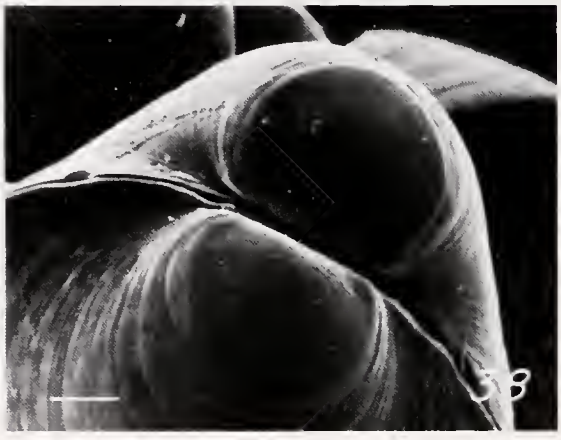


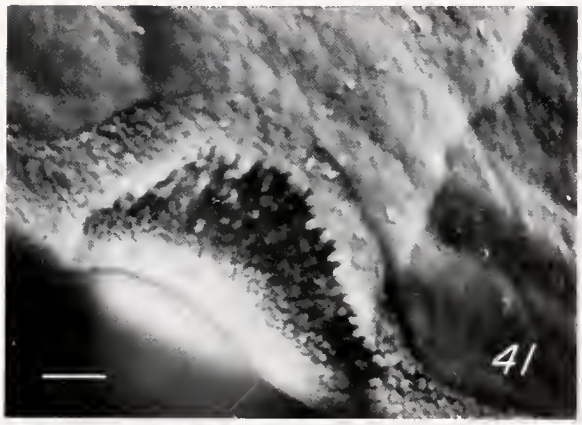
FIGURE 36. *Prodissoconch II, late pediveliger. Provinculum of left and right valves spread open showing anterior terminal teeth (t), outer ligament (l), cardinal socket (CS), and cardinal plateau (CP); inner larval ligament obscured by break. Scale bar = 20 μm.*

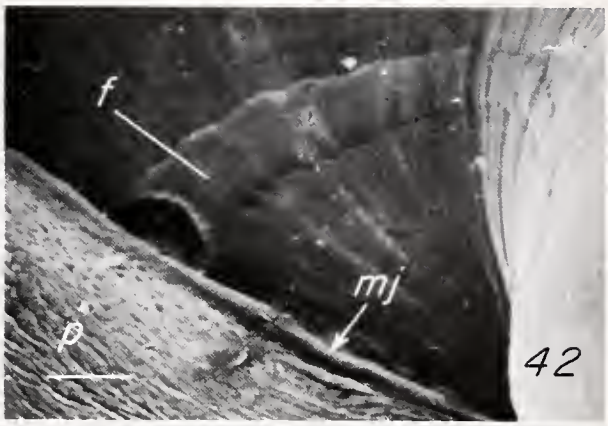
FIGURE 37. *Prodissoconch II, early stage. Posterior end of valves, fasciole (f) and notch (n) on left valve. 5% clorox 10 min. Scale bar = 20 μm.*

FIGURE 38. *Prodissoconch II, early pediveliger. Umbonal view of fasciole and notch on posterior side of left valve. 5% clorox 25 min, 6 min sonication. Scale bar = 20 μm.*

hinged area of the pivotal axis of the hinge (Figure 36).

An external shell structure, the fasciole, first described by Tanaka (1960), is located on the left valve (Figures 37 and 38) of prodissoconch II of *Crassostrea virginica*. The fasciole is a flattened, somewhat cornucopially shaped elevation of the surface of the shell (Figure 39). The fasciole arcs gracefully from the outer boundary of the prodissoconch I-II transitional band ventromedially





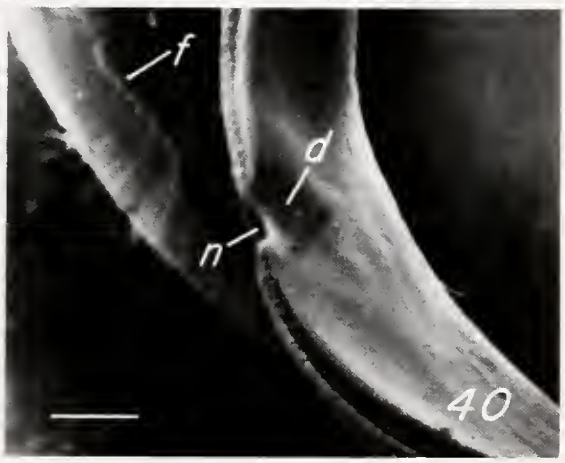


FIGURE 39. *Prodissoconch II, late pediveliger. Fasciole and notch. 5% clorox 45 min. Scale bar = 10 μm.*

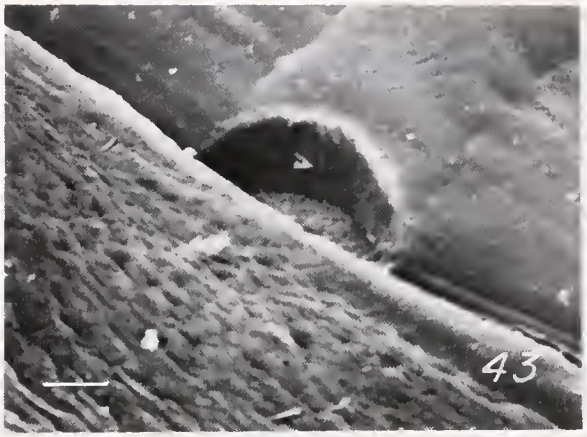
FIGURE 40. *Prodissoconch II, late pediveliger. Valve edge view of notch (n) (fasciole in background, f) and notch depression (d) on interior of valve. 5% clorox 45 min. Scale bar = 10 μm.*

FIGURE 41. *Prodissoconch II, late pediveliger. High magnification of fasciolar notch, end view. 5% clorox 45 min. Scale bar = 2 μm.*

FIGURE 42. *Dissoconch, early stage. Fasciole (f) and notch terminating at metamorphic juncture (mj) and beginning of prismatic (p) dissoconch shell. 5% clorox 30 min. Scale bar = 10 μm.*

to end abruptly at the metamorphic line between prodissoconch II and the spat (Figure 42). Aperiodic lateral extensions of the crest of the fasciole onto the surface of the shell are not closely correlated with the growth striae (Figures 39 and 42). The fasciole is solid and terminates at the prodissoconch II valve margin in a curved notch (Figures 39 and 41). A slight depression is reflected on the interior of the left valve opposite the fasciole and notch (Figure 40). Treatment of valves with 5% clorox for 45 min may have removed periostracum from the rim of the valve revealing the typically granular form of the shell units (0.2 to 0.4μm in diameter). Most of the periostracum on the remainder of the valve appears relatively untouched (Figure 41). The mature fasciolar notch (Figures 42 and 43), relatively resistent to the 5% clorox (30 min), is more smoothly curved than that in earlier stages of development (Figure 41). The ultrastructure of the new dissoconch shell adjacent to the notch is prismatic (Figure 43).

Valves of prodissoconch II larvae are surprisingly thin, ranging from 4 μm in the mid-pro-



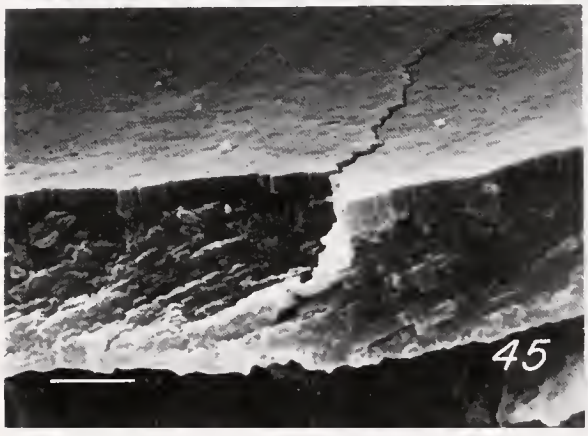


FIGURE 43. *Higher magnification of fasciolar notch shown in Figure 42. Scale bar = 4 μm.*

FIGURE 44. *Prodissoconch II, mid-stage. Fractured section of middle of valve, anteroposterior plane. Cleaned in 5% clorox 23 min, 3 min sonication before fracturing. Scale bar = 2 μm.*

FIGURE 45. *Prodissoconch II, pediveliger. Fractured section of middle of valve in dorsoventral plane. Cleaned in 5% clorox 25 min, 6 min sonication before fracturing. Scale bar = 3 μm.*

FIGURE 46. *Prodissoconch II, pediveliger. Fractured oblique section in dorsoventral plane, outer part of valve. Granules 0.2 to 0.5 μm in diameter. Cleaned in 5% clorox 45 min prior to fracturing. Scale bar = 2 μm.*

dissoconch stage (Figure 44) to 6 μm in a late pediveliger (Figure 45). The structure of the shell is homogeneous aragonite (Stenzel, 1964; Taylor et al., 1969), and it is composed of small granules ranging in diameter from 0.1 to 0.5 μm (Figures 44-46). There is a tendency for granules to be formed in columns (Figure 44), particularly in the inside layer. Granules are most conspicuous in the central part of the section (Figures 44 and 45), and different sizes of grains appear randomly mixed (Figure 46).

Early Dissoconch.

The abrupt change in the ultrastructure of valves from the homogeneous aragonite of the prodissoconch to the prismatic and foliated calcite of the dissoconch is striking (Figures 47, 48, and 50). Also prominent is the downward flaring of the left valve (Figure 49), facilitating its cementation to the substratum (Cranfield, 1973; 1974).

The outer layer of the right dissoconch valve is composed of prismatic calcite (Figures 50-52). Prisms increase in size from the metamorphic

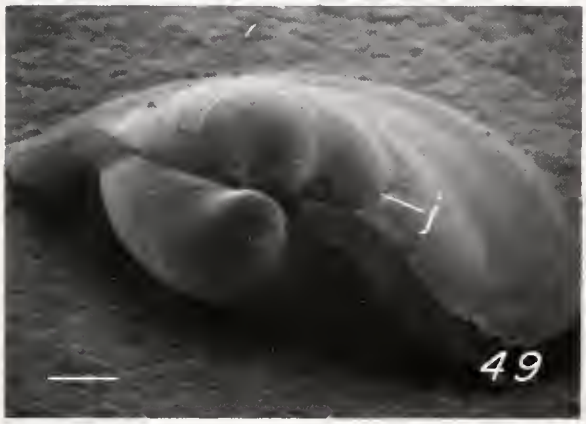


FIGURE 47. *Early dissoconch set on mylar film. 5% clorox 30 min. The clorox dissolved the fragile marginal matrix causing edge to crumble. Scale bar = 200 μm.*

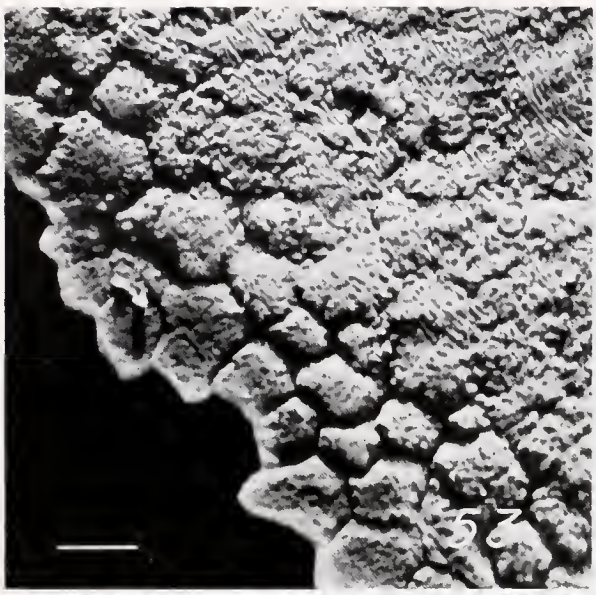
FIGURE 48. *Prodissoconch on early dissoconch valve. Sharp metamorphic line (mj). 5% clorox 60 min. Scale bar = 50 μm.*

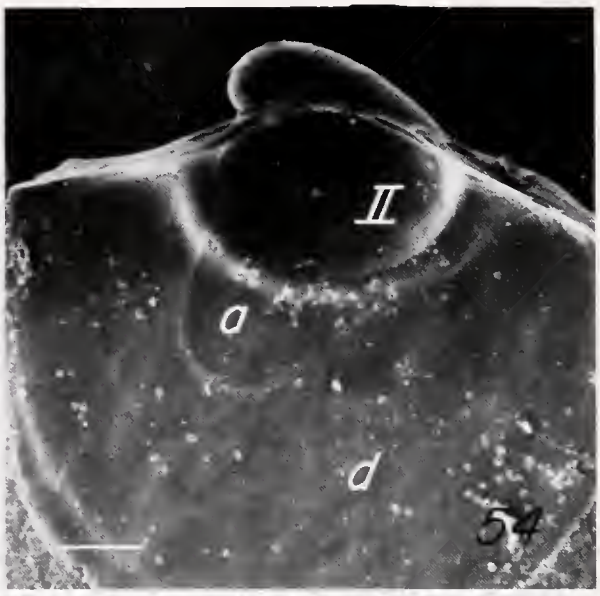
FIGURE 49. *Early dissoconch. Umbonal (dorsal) view to show juncture of prodissoconch II and dissoconch valves (j) and graceful downturning of spat valves onto mylar substratum. 5% clorox 30 min. Scale bar = 75 μm.*

FIGURE 50. *Higher magnification of metamorphic juncture shown in Figure 48. Homogeneous aragonite, prodissoconch valve (right); prismatic calcite, spat (left). 5% clorox 30 min. Scale bar = 15 μm.*

juncture toward the margin, reaching 9 to 11 μm in maximum surface dimension (Figures 50-52) in spat 31 days old and about 1 mm high. Their angular shapes are evident at the margin of the shell after treatment with clorox and gentle fracturing (Figure 52). Foliated calcite overgrows the interior surface of the right valve near the edge of the shell (Figure 53), partially eclipsing the characteristic pattern of the prisms. In this specimen the foliated calcite is of the chalky variety.

Except for a thin outer layer of prismatic calcite, and the aragonitic myostraca of muscle scars (Stenzel, 1971), the left dissoconch valve is composed of foliated calcite. At low magnifications the interior surface of the valve appears smooth, and the prodissoconch valve is clearly outlined beneath the foliated calcite (Figure 54), which is deposited over both the prodissoconch II valve and the dissoconch valve. The anterior adductor muscle develops first in the early veliger, and the posterior adductor appears in the early umboned





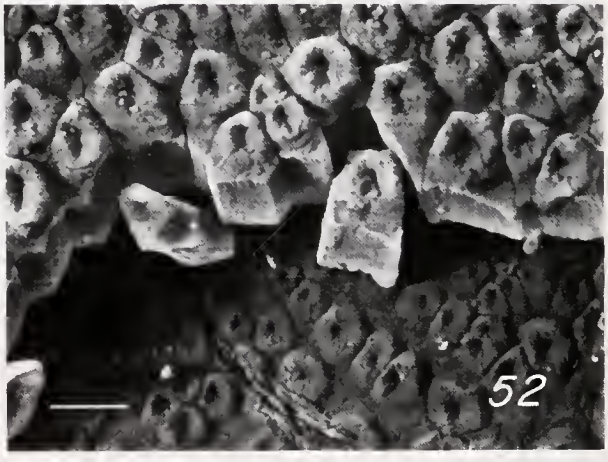


FIGURE 51. *Early dissoconch. Prisms on exterior surface of right valve in Figure 50, about midway between metamorphic line and ventrum. Scale bar = 6 μm.*

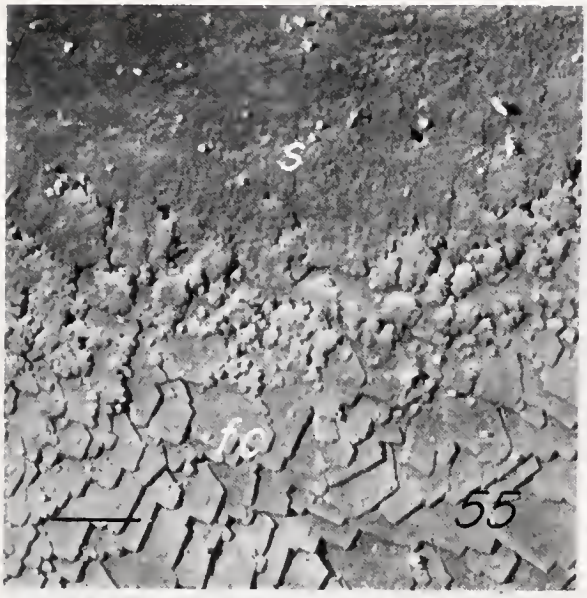
FIGURE 52. Early dissoconch. Prisms on exterior surface of right valve in imbricate scale at ventral edge of spat. Prisms in underlying scale smaller. 5% clorox 60 min. Scale bar = 8 μm.

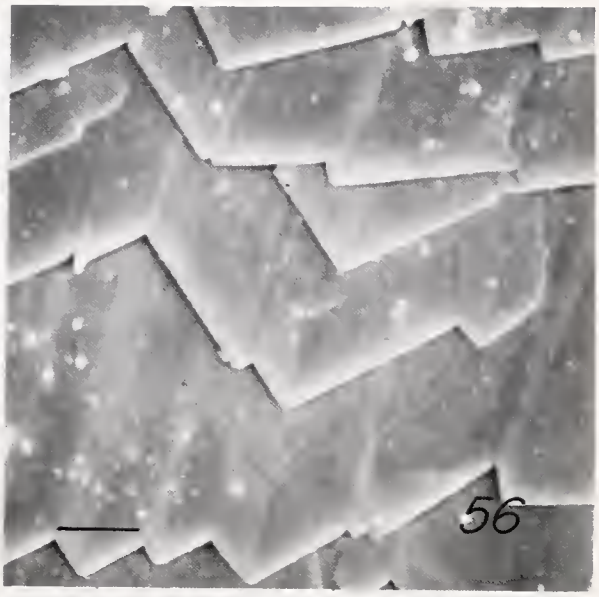
FIGURE 53. Early dissoconch. Prisms partially covered with foliated calcite of the chalky variety on interior surface near ventral margin of right valve. Prismatic edge has been knocked off. 5% clorox 60 min. Scale bar = 8 μm.

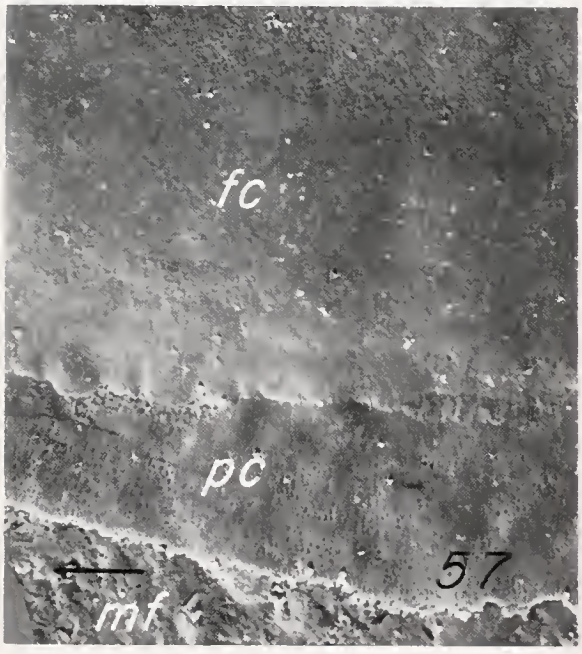
FIGURE 54. *Early dissoconch. Interior view of left valve on mylar film. Adductor muscle scar (a) straddles prodissoconch II (II) and dissoconch (d) shell. 5% clorox 30 min. Scale bar = 100 μm.*

larva. Following settlement, the anterior muscle is resorbed, and the posterior one moves anteroventrally to occupy its definitive position (Galtsoff, 1964; Stenzel, 1971). In the juvenile stage illustrated in Figure 54, the anterior adductor muscle scar has disappeared, and the posterior one has moved across the metamorphic juncture to its adult position.

Migration of the adductor muscle scar is accomplished by deposition of a thin myostracal







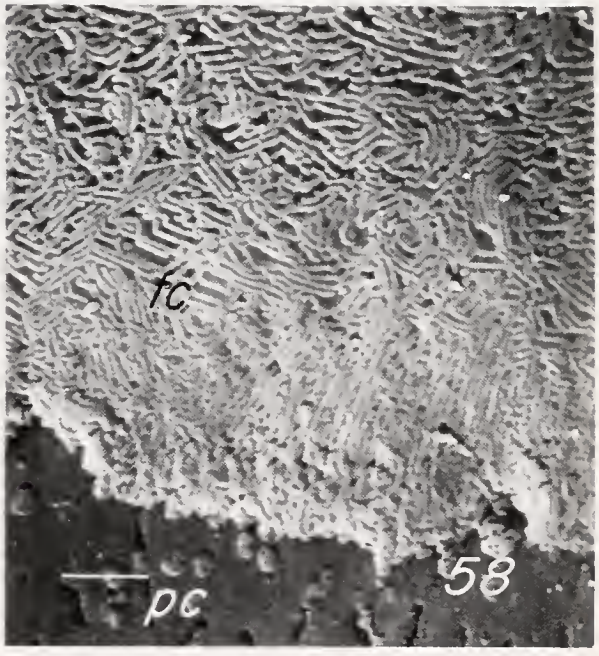
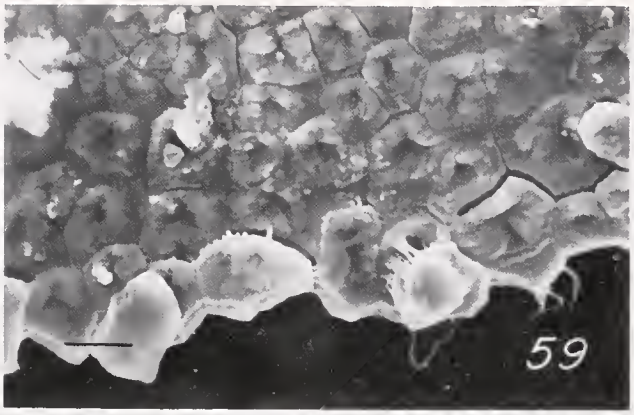


FIGURE 55. *Early dissoconch. Ventral boundary of adductor muscle scar (smooth myostracum, s) and foliated calcite (overlapping folia, fc). Same specimen as in Figure 54. 5% clorox 60 min. Scale bar = 7 μm.*

FIGURE 56. *Early dissoconch. Foliated calcite on interior surface of left valve. 5% clorox 30 min. Scale bar = 2 μm.*

FIGURE 57. *Early dissoconch. Ventral margin of left valve on mylar film. Outermost zone on mylar film (mf) is prismatic calcite (pc), and inner layer deposited over it is foliated calcite (fc). 5% clorox 60 min. Scale bar = 40 μm.*

FIGURE 58. *Higher magnification of Figure 57 at boundary of prismatic (pc) and foliated (chalky) (fc) structure. Scale bar = 4 μm.*



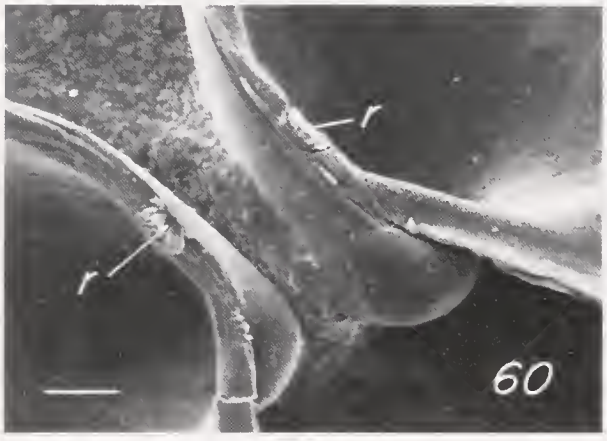


FIGURE 59. *Early dissoconch. Prisms, some partially dislodged, on interior surface of ventral margin of left valve. 5% clorox 30 min. Scale bar = 5 μm.*

FIGURE 60. *Early dissoconch. Opened matching pair of valves of spat showing resilium (r), one half in each chondrophore in hinge apparatus. Scale bar = 40 μm.*

FIGURE 61. *Enlargement of resilium in right valve in Figure 60. Scale bar = 8 μm.*

layer of shell over the surface of the foliated calcite in its path. The pattern of myostracal deposition is illustrated in Figure 55. This micrograph also illustrates the extreme smoothness of the surface of the myostracum to which the adductor muscle attaches. The rear (or dorsal) part of the myostracum, left behind as the scar migrates during shell growth, is covered by new layers of foliated calcite (Figure 54), and thus eventually becomes buried from surface view. A high magnification of the foliated calcite typical of the interior surface of valves shows the successive terrace-like layers of overlapping folia which in turn are composed of long thin laths whose boundaries are sometimes visible at the surface (Figure 56).

Shell of the left valve is secreted closely against the substratum (Figures 54 and 57). The outer layer is prismatic calcite (Figure 59), contrary to the report of Taylor et al. (1969) that in probably all species of oysters the outermost layer of only the right valve consists of simple calcitic prisms. Prisms are polyangularly cylindrical in shape, and comparable in appearance, but smaller in diameter, than those in the right valve (Figures 51 and 52). Deposition of foliated calcite follows close upon the prismatic layer (Figures 57 and 58), so that the prismatic zone is rather narrow and easily overlooked (Figure 57). The foliated calcite shown in Figure 58 is of the chalky variety.

At a dissoconch height of about 0.8 mm (Figure 54), the larval hinge apparatus with its heterodont teeth has become completely buried beneath

FIGURE 62. *Early dissoconch. Hinge area in left valve of spat showing resilium (r) in chondrophore, tensilia (t), and umbo of prodissoconch. 5% clorox 60 min. Scale bar = 4 μm.*

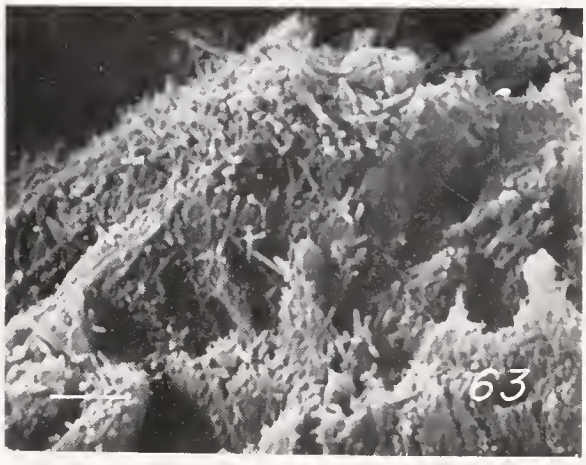


FIGURE 63. *Enlargement of calcareous fibers in resilium shown in Figure 62, exposed by treatment of the ligament with 5% clorox for 60 min, about 5 min of these at 60°C. Scale bar = 5 μm.*

dissoconch shell. The pivotal axis of the hinge has shifted from the center of the prodissoconch hinge anteriorly about 0.1 mm to the future center of the dissoconch hinge (Figure 60), the location of the inner larval ligament at the time of setting. The dissoconch hinge lacks teeth. At a spat height of 0.8 mm the inner ligament has grown to a block-shaped structure (the resilium, Galtsoff, 1964) about 30 μm wide (anteroposterior axis), supported in shallow chondrophores (Figure 60). Lateral extensions of the ligament, the tensilia, (Galtsoff, 1964) have began to form at this stage (Figure 62) and probably represent extensions of the outer ligament (Trueman, 1951). At a dissoconch height of about 1.8 mm the resilium is triangular in shape, fitting into a similarly shaped chondrophore in the hinge area of each valve (Figure 61). The inner width of the resilium is now about 75 μm, and broad flattened sheet-like tensilia have formed anteriorly and posteriorly between the opposing flat surfaces of the hinge nymphae (Figure 61) (Galtsoff, 1964). Tensilia are considerably thinner than the resilium. The resilium contains calcified fibrils (aragonitic according to Stenzel, 1962; Taylor et al., 1969; and confirmed by us), ranging in diameter from 0.3 to 0.4 μm, which are exposed by treatment with clorox (Figure 63). Tensilia lack calcified fibrils. Under compressive stress the resilium is strong, but under tension it is weak; tensilia are strong under bending stresses (Stenzel, 1971). In *Mytilus edulis* the aragonitic crystals of the ligament are enclosed in organic envelopes and are long, needle-shaped, single, and widely dispersed (Bevelander and Nakahara, 1969; Carriker, unpublished), somewhat similar to those in the oyster.

DISCUSSION

Comparison of larvae of *Crassostrea virginica* collected in estuaries (Carriker, 1951; 1959) and cultured in the laboratory (Carriker, 1959), or in a hatchery (College of Marine Studies), indicates that the external morphology is similar, and that confined culture, at least as seen at optical magnifications, does not seem to alter or deform the valves. This is reassuring, and suggests that larvae examined in this study probably had normally formed prodissoconch and early dissoconch valves.

Our finding that the polymorph of calcium carbonate in the valves of all prodissoconchs is aragonite confirmed Stenzel's (1964) report on prodissoconch II. Our results also demonstrated that larvae reared under hatchery conditions were identical mineralogically to those examined by Stenzel from another geographic region (Connecticut waters).

The striking punctate-stellate pattern on the exterior surface of the valves of prodissoconch I is probably associated with the shell-secreting activity of the developing shell gland and the circumferential spread of mineralization activity over the mantle epithelium of the veliger (Raven, 1966; Kume and Dan, 1968; see also LaBarbera, 1974). The process bears examination at cytological and ultrastructural levels. Ansell (1962) described, but did not illustrate, small punctate markings on the prodissoconch I valves of the bivalve *Venus striatula*.

According to Taylor et al. (1969), homogeneous shell structure is always aragonitic, and consists of minute calcium carbonate granules, all with similar crystallographic orientation. The crystallographic orientation of shell units of prodissoconch valves was not determined by us, but the larval shell is aragonitic, and ultrastructurally is composed of granules. In prodissoconch I valves the diameter of the granules ranges from about 0.05 to 0.1 μm, and in older prodissoconch II valves the diameter increases to a maximum of 0.4 μm. Accordingly, prodissoconch valves may be classified as homogeneous aragonite (Taylor et al., 1969). Whether the calcareous granules are formed in an organic matrix has yet to be determined.

As Stenzel (1971) pointed out, taxodont teeth of prodissoconch valves of common species of Ostreidae are larval structures only, and, as illustrated in this paper, are obliterated by the addition of new shell during the late prodissoconch II and early dissoconch stages. With the gradual functional loss of larval teeth, a more rapid process in the posterior ones (as also described for prodissoconchs of *Crassostrea angulata* [Pascual, 1971]), the pivotal axis of the hinge shifts to a position anterior to the umbones. The internal supportive function of the hinge apparatus is assumed by the dissoconch ligamental resilium, held securely in chondrophores, and by the tensilia, located between the broad lateral opposing nymphal surfaces. As illustrated by Ranson (1960), Galtsoff (1964), Stenzel (1971), and by us, the inner larval ligament is a distinct structure located anterior to the provinculum in the hinge apparatus of veligers. Pascual (1971) for *C. angulata* and Dinamani (1973) for *C. glomerata* noted that the "larval ligament" is also anterior to the provinculum in the prodissoconch of these species.

Stenzel (1971) suggested that the ligament, presumably the inner one, forms in the middle of the provinculum in the prodissoconch (at what stage is not indicated), so that the two valves open with opposing umbones remaining close together; as valves become more inequilateral and umbones more prominent, the ligament migrates smoothly and gradually along the hinge toward the anterodorsal valve margins, leaving umbones and larval teeth behind in their original positions. Our observations indicate, however, that the inner ligament forms anew anterior to the umbones where it later develops into the adult ligamental resilium. No inner larval ligament was observed by us inside the hinge between the terminal teeth. Tensilia, probably as extensions of the outer larval ligament, subsequently form to either side of the resilium. We concur with Trueman (1951) that the larval ligament at least in oysters is characteristic of the larval shell and the larval mode of life and that a different set of ligamental structures, evolving from the larval apparatus, are formed to meet the requirements of the post-larval shell.

A shift of the pivotal axis of the hinge, among other possible advantages, could permit wider gaping of the valves than would be possible were the pivotal point to remain at the closely apposed umbones. The point is provocative and raises the question whether, in the course of evolution, migration of the axis resulted because of the close juxtaposition of the large umbones or, conversely, evolution of the umbones to prominent features was made possible by shifting of the axis. A detailed study of the ontogenetic development of the ligament of oysters would shed further information on this interesting question.

No ligamental pit is evident at the site of the inner ligament in late veliger stages after the ligament has been removed with clorox. The absence of a depression is not unusual, as the adductor muscle, for example, attaches to ultrastructurally smooth myostracal surfaces.

The fasciole and notch, so characteristic of the left valve of prodissoconch II shells, were apparently first observed by Tanaka (1960) in *Saxostrea echinata* and seven other species, and recently, and independently, by Waller (1978) in

Ostrea edulis and by us in *Crassostrea virginica*. Pascual's (1971) light micrographs of larval valves of *Crassostrea angulata* suggest the presence of the fasciolar notch, but he makes no mention of it. The presence of this shell structure only in the prodissoconch II stage strongly suggests that it accompanies some function of a specialized part, or organ, of the mantle edge. The prominence of the fasciole and notch, and the depression of the interior surface of the valve in the vicinity of the notch, as well as increase in diameter of the fasciole as the larva grows, suggest that the organ is important to the veliger, possibly in some larval sensory function associated with feeding, swimming, or sensing light intensity. Since the fasciole terminates abruptly at the metamorphic juncture at the time of settlement, it is also possible the function of the organ, chemosensory or thigmosensory, or both, is related to searching by the pediveliger for a suitable settlement site and to subsequent cementation by the mantle edge and foot (Cranfield, 1973; 1974). Scanning electron microscopy of anesthetized, critical-point dried veligers of *Ostrea edulis* suggestsd to Waller (1978) that the notch is associated with a postanal ciliary tuft which propels water out of the mantle cavity. The potential importance of the organ in veliger and setting activities suggests further study of its structure and function.

The reason for the sharp transition at the metamorphic line from aragonitic homogeneous granules to foliated and prismatic calcite with islands of aragonite in myostracal muscle scars and resilial fibers (Stenzel, 1962, 1963, 1964; Galtsoff, 1964; Taylor et al., 1969) is still unclear. Unquestionably, the sudden structural change is associated with rapid metamorphosis from the motile pediveliger to the immobile spat; however, a more gradual transition than the sharp line of demarcation between the two types of shell might be expected.

Transition in shell structure, of course, could not occur without a change in the pattern of secretion of shell materials by the mantle epithelium. This means that epithelial cells, which in the larval stages were forming aragonitic granules, suddenly reconstitute themselves in the spat to secrete calcitic prisms at the rim of the valves. A further reconstitution occurs in the epithelium behind the valve edges where foliated calcite is secreted, in some places in the form of tightly packed laths, and in others as chalky shell with laths arranged in a spongy pattern. The ordered pattern of events which occurs in such rapid succession in young oysters are but manifestations of complicated biochemical processes and changes occurring at the cellular level, and a challenge to students of animal development (Raven, 1966). Lutz and Jablonski (1978) reported on the presence of a distinct prodissoconch-dissoconch boundary in the valves of juvenile late Cretaceous bivalves. Thus the process of rapid transition from larval to juvenile bivalves has been in existence over a long geologic period.

Why all, or nearly all, Bivalvia have aragonitic larval shells (Stenzel, 1964) is still unclear. Stenzel conjectures that aragonitic valves may be more advantageous than calcitic valves to motile veligers because aragonite is harder, has greater strength as a structural material, and is less prone to breakage by cleaving than calcite (see also Waller, 1975). Calcitic valves, on the other hand, may be more advantageous than aragonitic valves to bivalves which are permanently immobilized on the bottom, because calcite is less soluble in seawater and because it is secreted more economically than aragonite (calcite fills a larger volume per mole than aragonite) (Stenzel, 1964). Evolution of extreme thinness of larval valves may have been possible because of the structural characteristics of aragonite. The small mass of the valves facilitates suspension in the water column for the duration of the larval life history, and provides some mechanical protection from small predators and extreme abiotic conditions.

Our study has illustrated something of the ultrastructural complexity of the valves of young *Crassostrea virginica* and the developmental changes that occur in the shell during growth from the straight-hinge stage to the early spat. Results may be helpful to future investigators in the ultrastructural study and comparison of fossil and modern larvae (Lutz and Jablonski, 1978), systematic investigation of bivalve larvae employing fine structural features for diagnosis and identification (Chanley and Andrews, 1971), physiologic and embryologic study of shell formation (Raven, 1966; Kume and Dan, 1968), ex-

amination of erosional effects of laboratory and field environmental conditions on larval valve surfaces, recognition of abnormal ultrastructural shell formation, and investigation of the chemical composition of larval valve regions by such modern techniques as the proton microprobe.

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LITERATURE CITED

Ansell, A.D. 1962. The functional morphology of the larva, and the post-larval development of *Venus striatula* (da Costa). J. Mar. Biol. Assoc. U.K. **42**: 419-443.

Boyle, P.J. and R.D. Turner. 1976. The larval development of the wood-boring piddock *Martesia striata* (L.) (Mollusca: Bivalvia: Pholadidae). J. Exp. Mar. Biol. Ecol. **22**: 55-68.

Bevelander, G. and H. Nakahara. 1969. An electron microscope study of the formation of the ligament of *Mytilus edulis* and *Pinctada radiata*. Calc. Tissue Res. **4**: 101-112.

Carriker, M.R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr. **21**: 19-38.

Carriker, M.R. 1959. The role of physical and biological factors in the culture of *Crassostrea* and *Mercenaria* in a salt-water pond. Ecol. Monogr. **29**: 219-266.

Carriker, M.R. 1961. Interrelation of functional morphology, behavior, and autecology in the early stages of the bivalve *Mercenaria mercenaria*. J. Elisha Mitchell Sci. Soc. **77**: 168-241.

Chanley, P. and J.D. Andrews. 1971. Aids for identification of bivalve larvae of Virginia. Malacologia **11**: 45-119.

Cranfield, H.J. 1973. Observations on the behavior of the pediveliger of *Ostrea edulis* during attachment and cementing. Mar. Biol. **22**: 203-209.

Cranfield, H.J. 1974. Observations on the morphology of the mantle folds of the pediveliger of *Ostrea edulis* L. and their function during settlement. J. Mar. Biol. Assoc. U.K. **54**: 1-12.

Dinamani, P. 1973. Embryonic and larval development in the New Zealand rock oyster, *Crassostrea glomerata* (Gould). Veliger **15**: 295-299.

Dinamani, P. 1976. The morphology of the larval shell of *Saccostrea glomerata* (Gould, 1850) and a comparative study of the larval shell in the genus *Crassostrea* Sacco, 1897 (Ostreidae). J. Molluscan Studies **42**: 95-107.

Forbes, M. 1967. Generic differences in prodissoconchs of Gulf of Mexico oysters. Bull. Mar. Sci. **17**: 338-347.

Frazier, J.M. 1975. The dynamics of metals in the American oyster, *Crassostrea virginica*. 1. Seasonal effects. Chesapeake Sci. **16**: 162-171.

Frazier, J.M. 1976. The dynamics of metals in the American oyster, *Crassostrea virginica*. 2. Environmental effects. Chesapeake Sci. **17**: 188-197.

Galtsoff, P.S. 1964. The American oyster *Crassostrea virginica* Gmelin. Fishery Bull. Fish & Wildl. Serv. **64**: 1-480.

Giusti, F. 1973. The minute shell structure of the glochidium of some species of the genera *Unio*, *Potomida* and *Anodonta* (Bivalvia, Unionacea). Malacologia **14**: 291-301.

Imai, T., Ed. 1971 (1977). Biological research on the oyster. *In* Aquaculture in Shallow Seas: Progress in Shallow Sea Culture. Koseisha Koseiku Publishers, Tokyo. Translated from Japanese and published for NMFS and NSF by Amerind Publishing Co., New Delhi, p. 115-192.

Kobayashi, I. 1971. Internal shell microstructure of recent bivalvian molluscs. Sci. Rept. Niigata Univ., Ser. E, Geol. & Mineral., No. 2: 27-50.

Kume, M. and K. Dan. 1968. Mollusca. p. 485-537, *In* Invertebrate Embryology. Published for Nat. Libr. Med., Publ. Health Serv., and Nat. Sci. Found. by NOLIT, Publishing House, Belgrade, Yugoslavia.

La Barbera, M. 1974. Calcification of the first larval shell of *Tridacna squamosa* (Tridacnidae: Bivalvia). Mar. Biol. 25: 233-238.

Le Pennec, M. and M. Masson. 1976. Morphogenèse de la coquilli: de *Mytilus galloprovincialis* (Lmk.) élevé au laboratoire. Cahiers Biol. Mar. 17: 113-118.

Loosanoff, V.L. and H.C. Davis. 1963. Rearing of bivalve mollusks. Adv. Mar. Biol. 1: 1-136.

Lutz, R. and D. Jablonski. 1978. Larval bivalve shell morphometry: a new paleoclimatic tool? Science. 202: 51-53.

Magalhaes, H. 1948. An ecological study of snails of the genus *Busycon* at Beaufort, North Carolina. Ecol. Mongr. 18: 377-409.

Maurer, D. and K.S. Price. 1967. Holding and spawning Delaware Bay oysters *(Crassostrea virginica)* out of season. I. Laboratory facilities for retarding spawning. Proc. Nat. Shellfish. Assoc. 58: 71-77.

Milliman, J.D. 1974. Recent Sedimentary Carbonates. Marine Carbonates. Part 1. Springer-Verlag, Berlin. 375 p.

Nakahara, H. and G. Bevelander. 1971. The formation and growth of the prismatic layer of *Pinctada radiata*. Calc. Tissue Res. 7: 31-45.

Newkirk, G.F., L.E. Haley, D.L. Waugh and R. Doyle. 1977. Genetics of larvae and spat growth rate in the oyster *Crassostrea virginica*. Mar. Biol. 41: 49-52.

Palmer, R.E. and M.R. Carriker. 1979. Effects of cultural conditions on the morphology of the shell of the oyster *Crassostrea virginica*. Proc. Nat. Shellfish. Assoc. Vol. 69 See p. 58 in this vol.

Pascual, E. 1971. Morfologia de la charnela larvaria de *Crassostrea angulata* (Lmk.) en diferentes fases de su desarrollo. Investigacion Pesquera, Barcelona 35: 549-563.

Price, K.S., W.N. Shaw and K.S. Danberg. 1976. Proceedings of the First International Conference on Aquaculture Nutrition. Coll. Mar. Studies, Univ. Del. 323 p.

Pruder, G.D., E.T. Bolton, E.E. Greenhaugh and R.E. Baggaley. 1976. Oyster growth and nutrient nitrogen cost in bivalve molluscan mariculture. Univ. Del., Sea Grant Publ. DEL-SG-11-76, 20 p.

Ranson, G. 1960. Les prodissoconques (coquilles larvaires) des ostreides vivants. Inst. Oceanogr. Monaco, Bull. 57 (1183), 41 p.

Raven, C.P. 1966. Morphogenesis. The analysis of molluscan development. Pergamon Press, N.Y. 365 p.

Rees, C.B. 1950. The identification and classification of lamellibranch larvae. Hull Bull. Mar. Biol. 3: 73-104.

Richter, G. and G. Thorson. 1975. Pelagische Prosobranchier-Larven des Golfes von Neapel. Ophelia 13: 109-185.

Robertson, R. 1971. Scanning electron microscopy of planktonic larval marine gastropod shells. Veliger 14: 1-12.

Stanley, S.M. 1979. Aspects of the adaptive morphology and evolution of the Trigoniidae. Philos. Trans. Roy. Soc. Lond., B (in press).

Stenzel, H.B. 1962. Aragonite in the resilium of oysters. Science 136: 1121-1122.

Stenzel, H.B. 1963. Aragonite and calcite as constituents of adult oyster shells. Science 142: 232-233.

Stenzel, H.B. 1964. Oysters. Composition of the larval shell. Science 145: 155-156.

Stenzel, H.B. 1971. Oysters. Treatise on Invertebrate Paleontology. Part N, Vol. 3 (of 3), Mollusca 6, Bivalvia, N953-N1224.

Tanaka, Y. 1960. Identification of larva of *Saxostrea echinata* (Quoy et Gaimard). Venus 21: 32-38.

Taylor, J.D., W.J. Kennedy and A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea — Trigonacea. Bull. British Mus. (Nat. Hist.) Zool., Supplement 3: 1-125.

Thiriot-Quievreaux, C. 1972. Microstructures de coquilles larvaires de Prosobraches au microscope electronique a balayage. Arch. Zool. Exper. & Gen. 113: 553-564.

Togo, Y. 1977. The shell structure of the protoconch and the innermost shell layer of the teleoconch in marine prosobranch gastropods. J. Geol. Soc. Japan 83:567-573.

Trueman, E.R. 1951. The structure, development, and operation of the hinge ligament of *Ostrea edulis*. Quart. J. Microsc. Sci. **92**: 129-140.

Tsujii, T., D.G. Sharp and K.M. Wilbur. 1958. Studies on shell formation. VII. The submicroscopic structure of the shell of the oyster *Crassostrea virginica*. J. Biophys. Biochem. Cytol. **4**: 275-279.

Turner, R.D. and P. J. Boyle. 1974. Studies of bivalve larvae using the scanning electron microscope and critical point drying. Bull. Amer. Malacological Union **40**: 59-65.

Wada, K. 1963. Crystal growth of molluscan shells. Bull. Nat. Pearl Res. Lab., Kashikojima **7**: 703-828.

Waller, T.R. 1975. The origin of foliated-calcite shell microstructure in the subclass Pteriomorpha (Mollusca: Bivalvia). Bull. Amer. Malacological Union 1975: 57-58 (abstract).

Waller, T.R. 1976. The development of the larval and early post-larval shell of the bay scallop, *Argopecten irradians*. Bull. Amer. Malacological Union 1976: 46 (abstract).

Waller, T.R. 1978. Formation of a posterodorsal notch in larval oyster shells and the prodissoconch I/II boundary in the Bivalvia. Bull. Amer. Malacological Union 1978 (abstract) (in press).

Watabe, N. 1965. Studies on shell formation. XI. Crystal-matrix relationships in the inner layers of mollusc shells. J. Ultrastructure Res. **12**: 351-370.

Watabe, N., D.G. Sharp and K.M. Wilbur. 1958. Studies on shell formation. VIII. Electron microscopy of crystal growth of the nacreous layers of the oyster *Crassostrea virginica*. J. Biophys. Biochem. Cytol. **4**: 281-286.

Watabe, N. and K.M. Wilbur. 1961. Studies on shell formation. IX. An electron microscope study of crystal layer formation in the oyster. J. Biophys. Biochem. Cytol. **9**: 761-772.

Wilbur, K.M. 1972. Shell formation in mollusks, *in* M. Florkin and B. Sheer, ed., Chemical Zoology, Vol. 7, Mollusca. Academic Press, N.Y., p. 103-145.

Wilbur, K.M. 1976. Recent studies on invertebrate mineralization, *In:* N. Watabe and K.M. Wilbur, ed., The Mechanisms of Mineralization in the Invertebrates and Plants, Univ. North Carolina Press, p. 79-108.

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MACROBRACHIUM CULTURE IN THE UNITED STATES

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ABSTRACT

The United States has the honor of pioneering Macrobrachium *culture, thanks to the splendid work of Fujimura working in Hawaii from 1966 to the present; he used techniques elegantly worked out in the mid-sixties by Ling and modified them for extensive culture systems in large ponds. Fujimura also directs the Anuenue Fisheries Research Center in Hawaii that is dedicated to three main purposes:*

(1) help aquaculturists in the Hawaiian Islands establish economically viable culture systems,

(2) train investigators from the world community to be skillful and productive Macrobrachium *aquaculturists, and,*

(3) conduct basic research in Macrobrachium *biology, especially culture of larvae.*

Mulvihill began culturing Macrobrachium *in the late sixties in Florida; he has since allied himself with the Weyerhaeuser Company. The latter are presently searching systematically for a suitable electric generating station in this country in order to conduct a commercial-scale culture operation.*

Sandifer and Smith in South Carolina have made important contributions to Macrobrachium *culture, particularly in the areas of larval culture and nursery systems for culture of juveniles.*

Eble, Stolpe and Evans of Trenton State College working with Farmanfarmaian of Rutgers University and the Public Service Electric & Gas Company of New Jersey have developed techniques for intensive culture of Macrobrachium *using the waste-heat discharge waters of an electric generating station in New Jersey. Much emphasis has been placed on developing and refining nursery culture operations in which postlarvae are grown out to young juveniles in laboratory environments; Farmanfarmaian has also contributed much to our knowledge of physiology of late juveniles and adults, especially in areas of nutrition and stress.*

Culture of the giant Malaysian freshwater prawn, *Macrobrachium rosenbergii*, began in Malaysia and is in its infancy. We celebrate its twentieth anniversary this year. Ling and Merican (1961) first presented details of anatomy, life history and culture techniques. They discovered the fact that larvae require brackish water to complete their development, indicating that the genus has only recently migrated into fresh waters. Although over a hundred species of *Macrobrachium* exist in the world (Hedgpeth, 1949), the only serious culture has been conducted with M. *rosenbergii;* it grows rapidly to large sizes (35-50g are considered to be ideal for commercial harvest),

is quite disease resistant and adapts well to laboratory and pond environments alike. It should be noted that twenty-six species have been identified from the Americas (Holthuis, 1952); six of these are native to Florida.

In 1965, 36 freshwater prawns were shipped by Dr. Ling to Takuji Fujimura, associated with the Hawaii Department of Land and Natural Resources. Within the short span of six years, Fujimura (1971, 1972) had developed prawn culture into an economically viable industry. Further, his techniques in larviculture were so successful that his laboratory, the Anuenue Fisheries Research Center on Sand Island in Honolulu Harbor, became the center for distribution of prawns to laboratories throughout the world. In addition, the Anuenue Laboratory under "Fuji" (as he is known by workers in the field) attracted investigators from all over the world to study and learn all aspects of prawn culture techniques. This research work and world-wide educational service has been sponsored by the then U. S. Bureau of Commercial Fisheries, now the National Marine Fisheries Service, the National Sea Grant Program and the State of Hawaii.

Hawaii now has several commercial prawn farms in operation and is planning to add several hundred more acres in the next three years. Shang (1974) discussed the economic feasibility of freshwater prawn farming in Hawaii.

Early culture efforts on the U. S. mainland were confined to two laboratories in the State of Florida: Mr. Paul Mulvihill, Homestead and the Florida Department of Natural Resources, St. Petersburg. A detailed report concerning spawning and larval-rearing techniques of five species of *Macrobrachium* including *rosenbergii* was published by the latter (Dugan, Hagood and Frakes, 1975). More recently the St. Petersburg laboratory has conducted studies on mass culture of early juvenile prawns (M. *rosenbergii* and M. *acanthurus*) in protected nurseries using different diets (Willis, Hagood and Eliason, 1976). They stocked early juveniles (0.03g — average size) at 215, 430, 645 and 860 m^{-2} of bottom surface area. They obtained the best survival (52.4%) in the 2- month study in the 215 m^{-2}tanks; growth was only 0.108g during this period. By contrast, survival in the 860 m^{-2} tanks was 5.2%. Interestingly, this study showed trout chow (40% protein) to be an excellent ration for early juveniles (average conversion ratios for the first 30 days of the experiment were 1.31:1). Recent developments in prawn dietary formulations have taken advantage of these findings by doubling protein concentration of feed for early juveniles relative to adults (40% to 20%).

Prawn research and culture have been conducted at the Marine Resources Research Institute, Charleston, South Carolina for the past six years. Since the outdoor growing season is limited in this area to about five months (prawns stop growing below 18C; they die at 14C), much emphasis has been placed on development of nursery management systems in which postlarval prawns (0.03g) are grown to early juveniles (0.5g) preliminary to pond stocking. Willis and Berrigan (1977) demonstrated that a significant increase in pond production could be realized by stocking early juveniles (0.78g) as opposed to postlarvae; in approximately 165 days growing season, the former averaged 44g at harvest to only 29g for the latter. Percent survival was essentially the same for both groups (85%) as was food conversion ratios (1.6:1).

Sandifer and Smith (1977) stocked early juveniles (0.31g) at densities of 1,617 and 1,078 prawns m^{-2} tank bottom. Artificial substrate was added (7-cm wide strips of fiberglass window screening woven horizontally on a frame of vinyl coated wire and wood) to increase the total surface area of the tank volume (prawn larvae are pelagic but become benthic in habit after metamorphosis). In a 56-day growing experiment the authors noted no differences in either growth or percent survival between the two stocking densities: growth averaged 1.11g with 62% survival. The same authors (Sandifer and Smith, 1979) explored the economic potential of stocking various size prawns in pond grow-out trials in South Carolina. Three stocking strategies were employed: (1) postlarvae (0.1g), (2) 50:50 mixture of postlarvae and juveniles (1.2g) and (3) early juveniles (0.51g). All animal classes were stocked at 6.46 prawns m^{-2}; duration of the experiment was 153 days. While percent survival was essentially the same for all groups (73%), final size at harvest was 17.7g for prawns stocked as postlar-

vae compared with 23g for prawns stocked as a mixture of juveniles and postlarvae or juveniles alone. Gross production was 1,207 kg/ha for the ponds stocked with juveniles compared with only 840 kg/ha for those ponds stocked with postlarvae. This represented a 43% difference and resulted in a crop value differential of 65% since an increased number of larger class size prawns were available at harvest in those ponds stocked with juveniles or a mixture of juveniles and postlarvae.

In 1973, the Public Service Electric & Gas Co. (PSE&G), Rutgers University, Trenton State College, and the Long Island Oyster Farms began a long-range research effort exploring the potential of diseasonal waste-heat aquaculture. The original concept was to grow the freshwater prawn in outdoor ponds from mid-May to October and rainbow trout from November to the following May. The National Science Foundation — Research Applied to National Needs section — supplied the major portion of the funding; PSE&G also helped finance the project.

Waste-heat discharge waters, whether they originate from electric generating stations or other forms of industry, offer the aquaculturist two distinct advantages: (1) a plentiful supply of water (the Mercer Station discharges 1,892,500 l min^{-1}) and (2) the increase in temperature of the discharge water above river ambient (ΔT) extends the growing season of the species under cultivation.

Aquaculture laboratories and ponds were established at the Mercer Generating Station, a 550 megawatt coal-fired electric generating plant situated on the Delaware River in Trenton, N. J. All prawn experiments were directed towards high-density culture. Extensive culture methods developed by Fujimura (1971, 1972) in Hawaii dictated stocking ponds 10-15 postlarvae m^{-2}. Intensive culture methods developed by personnel at the Mercer Station (Eble, 1976; Eble, Stolpe, Evans and DeBlois, 1976, Eble, 1977) described stocking ponds at 36-54 juveniles m^{-2} pond bottom; ponds were supplied with artificial substrate in form of parallel rows of draped netting (Figure 1) to increase total surface area of pond volume. The shallow troughs formed between the parallel rows of netting were used by prawns for two purposes: molting and mating. Further, netting quickly became fouled with algae which added a supplementary source of prawn food as well as providing shade during daylight hours. Thus, two major changes from "traditional" (the tradition at this point was 6 years old) extensive culture methods were: (1) ponds were seeded with five times more prawns per unit area of bottom and (2) juveniles (1g) were stocked instead of postlarvae. Growth of prawns in three different shaped ponds (Figure 2) utilizing draped netting were essentially the same for the first 113 days (Eble, 1976); prawns were kept in the Raceway (Figure 2) for a total of 132 days and showed a final average weight of 18.9g as opposed to only 113 days in Pond I (13.5g) and Pond II (15g). These data show significantly higher pond production than both Willis and Berrigan (1977) and Sandifer and Smith

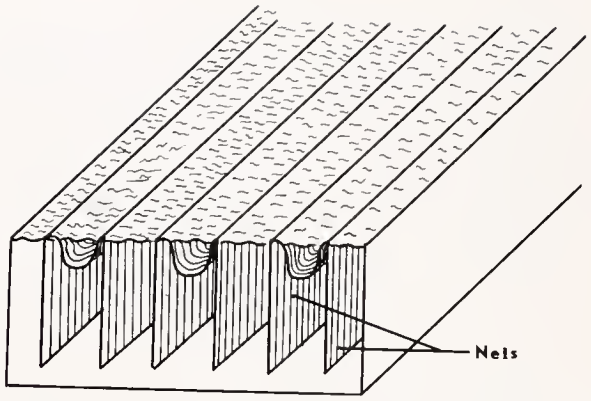

FIGURE 1. *Arrangement of draped netting to increase total surface area of pond volume. Prawns used shallow troughs (situated between long folds) for molting and mating.*

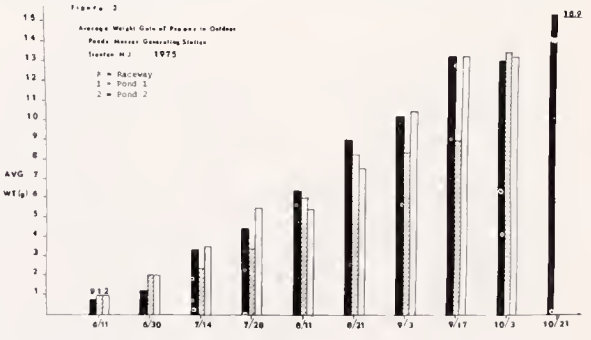

FIGURE 2. *Average weight gain of prawns in outdoor ponds, Mercer Generating Station, Trenton, N.J. 1975*

(1979): it should be noted, however, that both latter experiments employed extensive (low density) prawn stocking (Table 1). Although pond production was much higher in intensive-culture experiments it is significant that Willis and Berrigan (1977) doubled production by doubling the stocking density (Table I). Eble (1976) showed that even this latter figure could be doubled by taking advantage of the entire water column through the use of draped netting (Table I). The high feed conversions of the intensive system reflect the nature of the pond design and type of water flow characteristics: ponds were constructed with plastic liners and had no rooted vegetation; further, water was introduced at a sufficient rate to replace entire pond volume 5-8 times per day. Hence, no natural foods were available in ponds for prawn consumption (draped netting became fouled with algae and communities of invertebrates but this supplied only a minor component of total food supply for prawns). In contrast, the low-density, extensive systems reported here and elsewhere utilize water flows sufficient to just equalize evaporation. Phytoplankton blooms and macrophyte production are encouraged by enriching ponds with organic fertilizers and the low feed conversions reported (Table 1) in these extensive systems are a reflection of high pond production of natural foods for prawn grazing.

In short, pond production of prawns can be significantly increased by employing intensive (high density per volume) systems. High volumes of water flow must be used to supply oxygen and remove waste products (ammonia). This type system also precludes diurnal variation of temperature and dissolved oxygen; the latter is frequently a problem at night in extensive systems. Since little or no natural pond production is possible, prawns exist only upon food supplied daily to ponds and feed conversions are necessarily higher than those reported for extensive culture systems. Farmanfarmaian (1978), however, has improved the binding of Purina Marine Ration pellets which has substantially decreased the feed conversion when this material is used as the sole source of food; this investigator has also made significant contributions to prawn feed formulations by incorporating specific amino

TABLE 1. *Comparison Grow out Data Between Low Density and High Density Prawn Culture Methods*

Pond Data		Stocking Data			Harvest Data				
Designation	Area (m^2)	No. Prawns	Mean Size (g)	Density (#m^{-2})	Elapsed Days	Survival (%)	Mean Size (g)	kg/Ha	Feed Conversion
10[1]	181.44	840	0.760	5	167	68	48.7	1644.25	1.86:1
1[1]	186.64	933	0.051	5	171	83	26.1	1077.25	1.09:1
4[1]	240.48	2,265	0.051	10	166	68	17.9	1218.56	1.43:1
8[1]	199.24	3,788	0.063	20	169	73	14.4	2087.22	1.49:1
P1[2]	2,500.00	16,230	0.11	6.46	153	74	17.4	848.6	1.66:1
P&J1[2]	2,500.00	16,230	0.09	6.46	153	69	22.1	1157.2	2:33:1
			1.02						
			0.56						
J1[2]	2,500.00	16,230	0.51	6.46	153	78	22.7	1196.3	2.22:1
R[3]	75.60	4,052	0.7	54*	132	58	18.9	5835.05	7.4 :1
1[3]	226.80	11,230	0.7	54**	113	61	13.5	4077.38	7.7 :1
2[3]	225.00	8,346	1.0	36*	113	62	15.0	3416.00	6.7 :1

1 — Willis and Berrigan, 1977
2 — Sandifer and Smith, 1979
3 — Eble, 1976
* — Draped netting added to give prawn density — 20 m^{-2} total surface area (draped netting plus bottom)
** — Draped netting added to give prawn density — 27 m^{-2} total surface area (draped netting plus bottom)

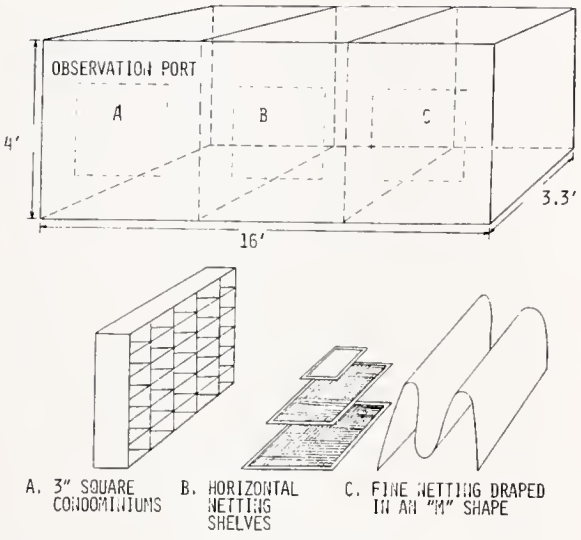

FIGURE 3. *Details of vertical substrate experiments with the wooden trough divided into three equal compartments, each containing a different substrate type.*

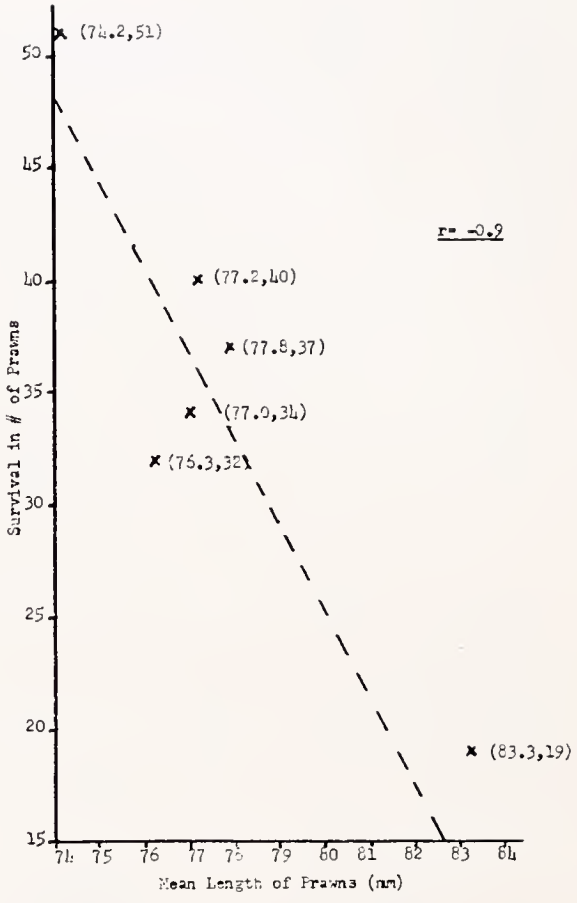

FIGURE 4. *Prawn survival vs. length.*

acids in prawn chow (Farmanfarmaian and Lauterio, 1979). Finally, with the use of waste-heat discharge water from an electric generating station in New Jersey (ΔT = 6C), the outdoor growing season for freshwater prawns can be increased by 30-45 days; to put this more graphically, the Mercer Station Aquaculture Laboratories are effectively "moved" from Trenton, N. J. to the vicinity of Charleston, S. C.!

Since the outdoor growing season for prawns was only 130-150 days at the Mercer Station a large-scale prawn nursery was established where postlarvae were grown to juveniles (lg) in two months preliminary to pond stocking. Larvae were grown at the Long Island Oyster Farms, Northport, N. Y. and, after metamorphosis, transferred to nurseries at the Mercer Station. Evans (1976), working at the Mercer Station, described methods of increasing the surface area of tank volume by use of artificial substrates (Figure 3). This same investigator established parameters for prawn length vs. survival as well as prawn length vs. density in nursery environments (Eble, Evans, DeBlois and Stolpe, 1977). Thus, investigators wishing to take advantage of prawn nursery techniques can predict survival of prawns as a function of size (Figure 4); further, they can stock nursery tanks with optimal numbers of prawns at each size range (Figure 5). Work is currently in progress at the Aquaculture Laboratories, Mercer Station, to extend this type data from postlarvae (12mm) to late juveniles (90mm).

It was predicted (Eble et al., 1977) that *Macrobrachium* aquaculture industries throughout the world will use nursery grow-out techniques within five years. The reasons are: (1) juveniles have an increased chance of survival in outdoor ponds; (2) slow-growing postlarvae can be artificially selected against, thus only fastest growing animals are stocked in ponds; (3) juvenile nurseries can be managed better than ponds; (4) outdoor growing seasons can be shortened by 40-50%.

Recent work at the Aquaculture Laboratories at the Mercer Station has concentrated on grow-out

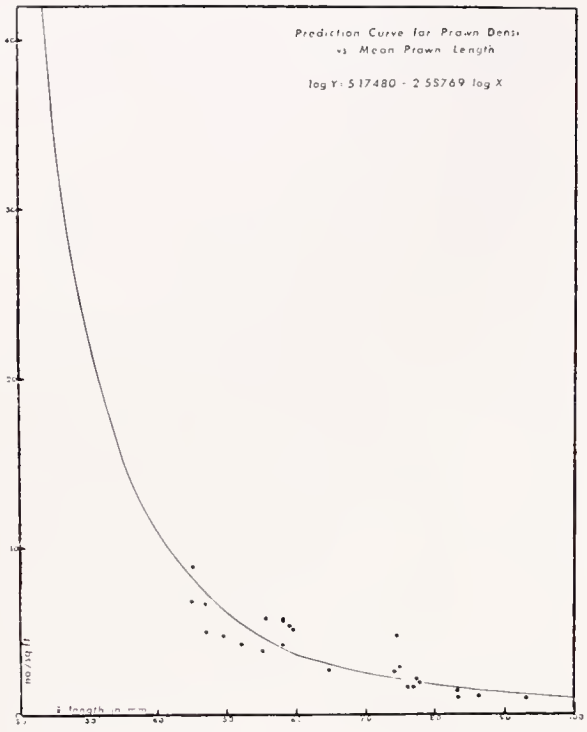

FIGURE 5. *Prawn density vs. length.*

of juvenile prawns in closed cells or compartments (Figure 6). These structures (called "condominiums" in our laboratory) are similar in design to egg crates; individual compartments are completely isolated from each other effectively preventing prawn interaction (Stolpe, 1976). Size of compartments presently under investigation range from 5.08 x 5.08 x 20.32cm to 10.16 x 10.16 x 20.32cm. Preliminary results indicate a direct relationship in growth and an inverse relationship in mortality with size of compartment.

Condominiums are placed in series in rectangular tanks and supplied with fast-flowing water from a semi-closed system (Figure 7); condominiums are constructed on the plan of arhombus when viewed from the side which facilitates feeding since food scattered from the surface of the

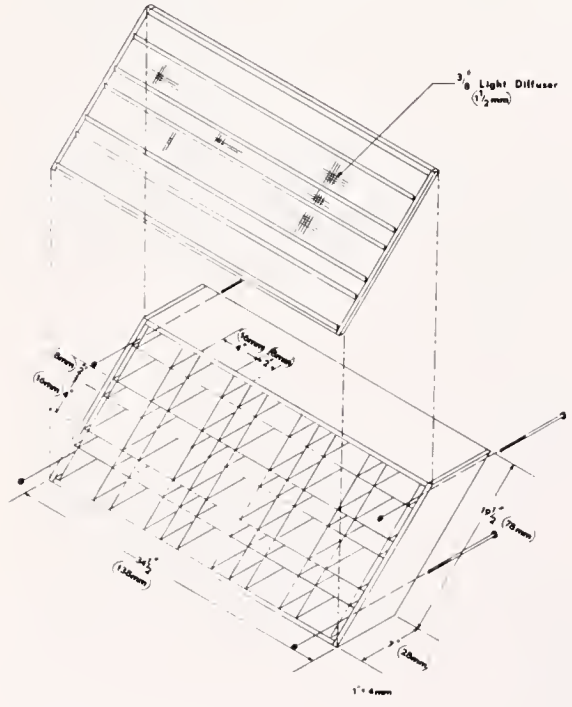

FIGURE 6. *Closed cells.*

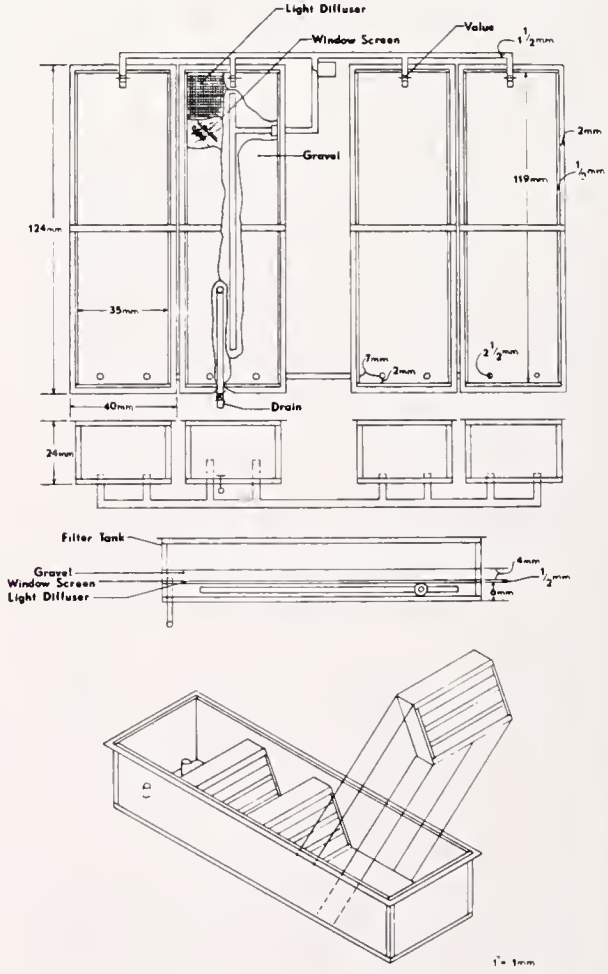

FIGURE 7. *Closed cell filter & tank arrangement.*

tank will settle equally on all feeding shelves.

Growing prawns in closed compartments offers many advantages: (1) eliminates cannibalism; (2) eliminates dominance effect of larger animals over smaller ones; (3) allows for more efficient use of water column (prawn density could range between 318 - 565 prawns m^{-3}); (4) facilitates harvesting.

Recently, the Weyerhaeuser Company has taken over management of the Mulvihill prawn farm in Homestead, Florida. A large-scale hatchery is in use and postlarvae are presently being shipped all over the world. This company is presently evaluating sites both in the United States and abroad for a commercial-scale prawn farm.

Macrobrachium rosenbergii has been under cultivation for only 12 years. Much work has been accomplished by many investigators in the field (Hanson and Goodwin, 1977) and the future for prawn culture is bright and promising. The day has already passed when we can reap our harvests from natural production in oceans, bays and freshwater environments. The age of agriculture started 10,000 years ago; the age of aquaculture is just dawning. Each year will see a greater portion of protein produced to feed a hungry world coming from cultivated sources, both agri-and aquaculture. Prawn farming will constitute an important role in this production of protein.

LITERATURE CITED

Degan, C. C., R. W. Hagood and T. A. Frakes. 1975. Development of spawning and Mass Larval Rearing Techniques for Brackish-Freshwater Shrimps of the Genus *Macrobrachium* (Decapoda, Palaemonidae). Flor. Mar. Res. Publ. No. 12: 1-28.

Eble, A. F. 1976. Integration of Thermal and Food Processing Residuals into a System for Commercial Culture of Freshwater Shrimp (Power Plant Waste Heat Utilization in Aquaculture). Final Report, July 1974-76. NSF/RANN AEN 74-14079 and GI-43925.

Eble, A.F., N. E. Stolpe, M. C. Evans and N. F. DeBlois. 1976. The Use of Thermal Effluents of an Electric Generating Station in New Jersey in the Culture of the Tropical Prawn, *Macrobrachium rosenbergii*, and the Rainbow Trout *Salmo* gairdneri, pp. 47-55. in, Power Plant Waste Heat Utilization in Aquaculture —Workshop I Papers. ed. by C. R. Guerra, B. L. Godfriaux and A. F. Eble. Public Service Electric & Gas Co., Newark.

Eble, A. F. 1977. Powerplant Waste Heat Utilization in Aquaculture. First Ann. Rep. Nov. 1977. NSF/RANN Grant ENV 76-19854 AO1, PSE ' G Grant Ro-443.

Eble, A. F., M. C. Evans, N. F. DeBlois and N. E. Stolpe. 1977. Maintenance of Brood Stock, Larval Rearing and Nursery Techniques used to Grow *Macrobrachium rosenbergii* in Waste-Heat Discharge Waters of an Electric Generating Station in New Jersey (U.S.A.) Actes de Colloques du C.N.E.X.O. 4:233-245.

Farmanfarmaian, A. 1978. Powerplant Waste Heat Utilization in Aquaculture. Second Ann. Rep. Nov. 1978. NSF/RANN Grant ENV 76-19854 AO1, PSE&G Grant RO-443.

Farmanfarmaian, A. and T. Laurterio. 1979. Diseasonal Thermal Aquaculture: Amino Acid Supplementation of Feed Pellets of the Giant Shrimp, *Macrobrachium rosenbergii*. in press, Proc. 10th Ann. Meet. World Mariculture Soc.

Fujimara, T. 1971. Development of a Prawn Culture Industry. Statement of Project Accomplishments. Hawaii Sub-Project H-14-D-1. Am. Rep. to Bur. Comm. Fish., U.S. Dept. Int. 6pp.

1972. Development of a Prawn Culture Industry. Statement of Project Accomplishments. Hawaii Sub-Project H-14-D-1. Ann. Rep. to Bur. Comm. Fish., U.S. Dept. Int. 6 pp.

Hanson, J. A. and H. L. Goodwin. 1977. Shrimp and Prawn Farming in the Western Hemisphere. Dowden, Hutchinson & Ross, Inc. Stroudsburg. 439pp.

Hedgpeth, J. W. 1949. The North American species of *Macrobrachium* (river shrimp). Texas J. Sci. 1 (3): 28-38.

Holthuis, L. B. 1952. The Subfamily Palaemoninae. A General Revision of the Palaemoninae (Crustacea, Decapoda, Natantia) of the Americas, II. Occ. Pap. Allan Hancock Found. 12: 1-396

Ling, S. W. and A. B. O. Merican. 1961. Notes on the Life and Habits of the Adults and Larval Stages of *Macrobrachium rosenbergii* (De Man). Indo-Pac. Fish. Counc. Proc. 9 (2): 55-61.

Sandifer, P. A. and T. I. J. Smith. 1977. Intensive Rearing of Postlarval Malaysian Prawns *(Macrobrachium rosenbergii)* in a Closed Cycle Nursery System. Proc. 8th Ann. Meet. World Mariculture Soc. 225-235.

Sandifer, P. A. and T. I. J. Smith. 1979. Development of *Macrobrachium* Aquaculture in South Carolina. Sea Grant Project Summary, Project No. R/A-1. 28pp.

Shang, Y. C. 1974. Economic Feasibility of Freshwater Prawn Farming in Hawaii. Sea Grant Ad. Rep. UNIHI-SEA GRANT-AR-74-05. 49pp.

Stolpe, N. E. 1976. Prawn Compartmentalization Experiments I, II, in, Integration of Thermal and Food Processing Residuals into a System for Commercial Culture of Freshwater Shrimp (Power Plant Waste Heat Utilization in Aquaculture). Final Report, July 1974-76. NSF/RANN AEN 74-14079 and GI-43925.

Willis, S. A., R. W. Hagood and G. T. Eliason. 1976. Effects of Four Stocking Densities and Three Diets on Growth and Survival of Postlarval *Macrobrachium rosenbergii* and M. *acanthurus*. Proc. 7th Ann. Meet. World Mariculture Soc. 655-665.

Willis, S. A. and M. E. Berrigan. 1977. Effects of Stocking Size and Density on Growth and Survival of *Macrobrachium rosenbergii* (De Man) in Ponds. Proc. 8th Ann. Meet. World Mariculture Soc. 251-264.

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WATER QUALITY IN SHELLFISH CULTURE

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ABSTRACT

Water quality is a basic, yet all-important factor in the operation of a mariculture facility regardless of location, design, or species being cultured. The water must conform to the requirements of the species being raised with regard to temperature, pH, salinity ranges, and metabolic wastes. In addition, the water must be free of pathogenic microbes and chemical contamination, yet contain adequate nutrients and dissolved oxygen to nourish the cultured species.

A mariculture facility permits the control and enhancement of culture water through screening and examination of intake waters, disinfection methods, and the use of thermal and nutrient additives.

INTRODUCTION

The necessity of employing water of suitable quality in aquaculture operations appears academic. However, investigation reveals that while the water available to a mariculture facility may be capable of supporting shellfish growth and reproduction, it may not be acceptable for culture of an edible consumer product.

Bivalve mollusks can accumulate viruses, bacteria, heavy metals, radionuclides, and pesticides from contaminated seawater and act as vectors of typhoid fever, infectious hepatitis, and *Salmonella*-related enteric infections. Under certain conditions, some mollusks can also concentrate toxins, such as paralytic shellfish poison, rendering the mollusk poisonous to vertebrates, including man. In addition, other phytoplankton metabolites released during seasonal blooms may interfere with growth and development of shellfish larvae and prevent spawning of adults.

Therefore, the successful operation of a mariculture facility depends upon the delineation of the physical and biological parameters of the water used in the facility. Those water characteristics known to ensure optimal growth of the species being cultured can then be supplied, if they are lacking, and steps may be taken to correct any existing contamination problems.

Water Quality Parameters

There are five major water characteristics which determine growth in shellfish: temperature, salinity, available nutrients, pH, and dissolved oxygen.

Temperature is of vital importance in shellfish culture as it determines the survival of a species in an area, controls growth rates, and regulates reproductive activity (Loosanoff and Davis, 1963). Alexander (1968) listed temperature, salinity, and available nutrients as primary factors in the success of oyster culture. Butler (1965) examined the effects of salinity, pH, nutrient salts, dissolved copper, chlorophyll, total plankton, turbidity, and currents on shellfish growth. He reported that salinity controlled the distribution of oyster populations in an estuarine system, as well as the market value. In a later paper, Glude (1978) agreed with these observations.

A series of experiments in which temperature, salinity, and nutrients were controlled demonstrated the importance of available nutrients in seawater to shellfish growth (Shaw, 1967). In this investigation shellfish meat quality (percent solids) was shown to be greater in raw seawater than in artificial ponds due to the lack of algal food in the latter.

Glude (1978) indicated that the successful operation of all aquaculture facilities, especially those which recycle water, depends upon the detoxification of ionized (NH_4) and unionized (NH_3) ammonia. Unionized ammonia is more toxic to most cultured species than the ionized form. However, oysters and clams have high tolerances to ammonia, exhibiting an LC_{50} of 100 mg/l in a 96-hour ammonia exposure. Glude also reported that shellfish have fairly wide ranges of pH tolerances but achieve optimal growth within a narrow range (i.e., *Crassostrea virginica* tolerates a pH range of 6.75-8.75 but best yields are obtained from pH 8.25-8.50).

Bardach et al. (1972) noted that dissolved oxygen levels must be adequate to insure good yields in mariculture at each developmental stage. For example, adult oysters require dissolved oxygen levels of 1.0-2.5 mg/l, but larvae need 4.0 mg/l to survive.

The water characteristics mentioned above can be affected quickly and are greatly altered by storms, human and industrial contamination, and metabolic wastes. Water parameters are, therefore, highly variable and subject to both natural and man-made fluctuations (Neilson et al., 1978; Zoellner, 1977).

Water Quality Control

Water Disinfection

Culture species and available water supplies should be correlated so that the greatest yields in production and economic value may be realized. However, in view of the many factors affecting water quality, water sources available for mariculture purposes can be contaminated biologically or chemically by substances hazardous to the successful operation of the facility.

The shipment of shellfish seed stock across continents, which previously prevented natural dissemination of shellfish species and their parasites, has further served to contaminate breeding waters with pathogens (Key, 1977; Sindermann, 1970). Due to uncontrolled transfer, Japanese seed oysters spread a parasitic copepod, *Mytilicola orientalis*, and two other disease organisms to the United States west coast shellfisheries. The U.S. east coast has also been affected by the free transfer of shellfish containing MSX (*Minchinia* sp.) and *Dermocystidium* organisms which rapidly invaded new niches and infected most major breeding grounds. As a result, several states, i.e., Washington, Maine, New York, Maryland, Delaware, and Hawaii, now have restrictions on exotic shellfish imports and intrastate transfers of native shellfish. However, smuggling and illegal transfer of shellfish frequently occur due to conflicting state regulations (Office of Fisheries Development, 1977) and the problem of parasite introduction to "clean" waters remains a threat.

A distinct advantage of a mariculture operation is that water quality may be accurately controlled despite the conditions existing at the water source. Culturing may be of great importance when one considers that the collection of oysters (*C. virginica*) on the Atlantic coast of the United States was reduced from more than 43 million kg in 1920 to less than 21 million kg in 1964 (Bardach et al., 1972). Similarly, a fivefold decrease occurred in the harvest of the blue mussel (*Mytilus edulis*) in the United States between 1946 and 1947 (pers. commun.[1]). These reductions were attributed in part to pollution and poor resource management, both of which can be avoided in a mariculture operation if disinfection procedures are routine features of the facility's operational plan. Routine monitoring of the water quality must be conducted to detect any problems with the intake water or with the water used throughout the culture cycle.

In a closed-cycle mariculture system, as opposed to the traditional rafting or hatchery-harvest techniques, problems with water quality variability are reduced though not entirely absent. Most closed-cycle operations to date still require a 10% water replacement to complete the cycle

[1] R. Lutz, Yale University, New Haven, CT 06520

(Booda, 1977; Pruder et al., 1977), which may introduce contaminants.

In the event of a water contamination problem or in an area where the water must always be treated before use, several means of disinfection are available which vary in application methods, expense, and successful use. These methods include the use of ozone gas bubbled through the culture water (Blogoslawski and Stewart, 1977; Blogoslawski, 1977); ultraviolet light (Blogoslawski et al., 1978; Brown, 1979); antibiotics (Pennec et al., 1973); and chlorine (Dodgson, 1928). The use of one or more of these systems prevents biological contamination of the cultured stock and the resulting economic losses.

The Use of Thermal and Nutrient Additives

The possibility of using waters which are thermally heated by power plants for out-of-season spawning and for the growth of shellfish in a mariculture facility is an example of using existing water conditions to facilitate production. The following two recent experiments indicate increased yields in heated waters and that the use of these effluents would allow a longer growing season in northern waters for temperate and tropical species. A New Jersey Public Service Electric and Gas study (1977) suggested that aquaculture using thermal additions could become a 0.5 billion dollar/year industry if approximately 10% of the fossil fuel effluents were used for propagation of trout or catfish.

Eble et al. (1977) reported that use of heated discharge waters from power stations would allow mariculture stations to operate as if they were located between 7-12° latitude toward the equator. The higher water temperature, then, would permit commercial production of tropical species in northern and southern temperate zones.

Recently, concern has been expressed over the introduction of heavy metals and radionuclides into natural waters from power plant effluents. Carlberg and Van Olst (1977) reported that the condenser cooling system of three fossil fuel generating stations did not affect the concentration of heavy metals in the effluent water or in the animals exposed to the heated effluent. The concentrations of the metals in all tissues examined were well below the limits established by the Food and Drug Administration for edible consumer products.

Price et al. (1976) reported a seasonal advantage gained by using thermally heated waters from a nuclear power plant. The heat provided by the plant increased the temperature of the water sufficiently to allow the *C. virginica* located in the warmer sites to take advantage of the increased food available in the early spring. They also described a schedule for harvesting which would minimize the concentration of radionuclides found in the oysters. Systems must be developed to prevent contact of contaminated waters with shellfish in hatchery nursery and grow-out systems.

Enhanced growth of culture organisms has also been achieved through the use of sewage-contaminated water as enrichment fertilizer in aquaculture systems (Bardach et al., 1972). Closed-cycle systems provide mariculturists flexibility in using contaminated water under quarantine or in using clean water far from a marine source (MIT Marine Industry Collegium, 1977).

Mann and Ryther (1977) reported that *Crassostrea gigas*, *Tapes japonica*, and *Ostrea edulis* grew well between 15-20° C on sewage-fertilized seawater containing mostly *Phaeodactylum tricornutum* at 10^4 cells/ml. However, *Mercenaria mercenaria*, *Mytilus edulis*, and *Crassostrea virginica* showed poor growth under these experimental conditions. Mann (in press) later reported that the *Mytilus edulis* growth rate was significantly better (116% increase in live weight) over Mann and Ryther's (1977) earlier study due to the use of 14°C seawater and a predominance of *Skeletonema costatum* (10^5 cells/ml) over *Phaeodactylum tricornutum* in secondary effluent-enriched seawater.

Some of the success of rearing shellfish in polluted waters may be explained by the work of Fankboner and de Burgh (1978) who suggest that dissolved organic carbon (DOC) is accumulated by juveniles of *Crassostrea gigas* as food. Thus, phytoplankton food sources may be supplemented by addition of specific organic nutrients to preveliger stages of bivalves. These data seem to bear out the poor growth observed of *C. virginica* larvae grown experimentally in activated carbon-filtered seawater with the correct concentration of unialgal food. It is obvious, however, that much

additional basic research is needed before a complete understanding of sewage enrichment is known and made commercially feasible (unpublished observation).

SUMMARY

The successful operation of a shellfish culture facility requires that the water quality be suited to the species being raised. Physical characteristics, such as temperature, salinity, pH, and dissolved oxygen, should correspond to those parameters found to provide optimal growth for the cultured species. In addition, an adequate supply of required nutrients is of importance.

The potential for using existing water conditions should not be overlooked in shellfish culture. Heated effluents from power plants can cause temperate species (i.e., *Crassostrea virginica*) to increase their growth rates and extend their growth periods. Similarly, the potential for using nutrient-rich waters from sewage plants in carefully controlled applications is being explored. Thus, waters need not be of pristine quality to be regarded as optimal growth media (FAO, 1974). From an economic standpoint, perhaps species should be matched to individual sites which would require the least alteration to provide optimal growth.

Waters which are otherwise suitable for mariculture purposes, however, are often microbially or chemically contaminated. Whether induced by man or of natural origin, water pollution is a principal barrier to the development of mariculture. Contamination and disease of stock resulting from pollution can occasion devastating and irrevocable economic losses. In areas where mariculture operations must draw their water from contaminated sources, the most thorough methods of seawater disinfection should be routinely employed. To avoid the spread of shellfish pathogens, quarantine techniques must be developed to take advantage of selected exotic species traits.

Water quality is a most important determinant of the success of a mariculture venture. Greatest success can be achieved by knowing the growth parameters and requirements of the shellfish to be cultured throughout their life cycles and providing a water supply meeting these needs.

LITERATURE CITED

Alexander, J. E. 1968. Water quality and the growth of oysters. *In:* Clarke Williams (ed.), Proceedings of the Conference on Shellfish Culture. Sponsored by the Regional Marine Resources Council, Nassau-Suffolk Planning Board and the Suffolk Community College, pp. 33-38.

Bardach, J. E., J. H. Ryther, and W. O. McLarney. 1972. Aquaculture. Wiley Interscience, New York. 868 pp.

Blogoslawski, W. J. 1977. Ozone as a disinfectant in mariculture. *In:* Proceedings of the Third Meeting of the I.C.E.S. Working Group on Mariculture, Brest, France. Actes Colloq. C.N.E.X.O, 4:371-381.

Blogoslawski, W. J. and M. E. Stewart. 1977. Marine applications of ozone water treatment. *In:* E. G. Fochtman, R. G. Rice, and M. E. Browning (eds.), Forum on Ozone Disinfection. International Ozone Institute, Syracuse, New York, pp. 266-276.

Blogoslawski, W. J., M. E. Stewart, and E. W. Rhodes. 1978. Bacterial disinfection in shellfish hatchery disease control. *In:* James W. Avault, Jr. (ed.), Proceedings of the Ninth World Mariculture Society Meeting, Louisiana State University, Baton Rouge, LA., pp. 589-602.

Booda, L. L. 1977. Oysters grown in Kansas City? Sea Technol.18(6):16-20.

Brown, C. 1979. Ultraviolet light: an effective disinfectant for shellfish hatcheries? Ozonews, International Ozone Institute, Cleveland, Ohio, 6(2): 6-7.

Butler, P. A. 1965. Reaction of estuarine mollusks to some environmental factors. *In:* Third Seminar, Biological Problems in Water Pollution. U. S. Dep. Health, Educ., Welf. No. 999-WP-25:99-104.

Carlberg, J. M. and J. C. Van Olst. 1977. Methods for culturing the American lobster (*Homarus americanus*). *In:* Proceedings of the Third Meeting of the I.C.E.S. Working Group on Mariculture, Brest, France. Actes Colloq. C.N.E.X.O. 4: 261-275.

Dodgson, R. W. 1928. Report on Mussel Purification. Fish. Invest. Series 2, 10(1):296.

Eble, A. F., M. C. Evans, N. Deblois, and N. E. Stolpe. 1977. Maintenance of brood stock, lar-

val rearing, and nursery techniques used to grow *Macrobrachium rosenbergii* in waste-heat discharge waters of an electric generating station in New Jersey (U.S.A.). *In:* Proceedings of the Third Meeting of the I.C.E.S. Working Group on Mariculture, Brest, France. Actes Colloq. C.N.E.X.O. 4:233-245.

Fankboner, P. V. and M. E. de Burgh. 1978. Comparative rates of dissolved organic carbon accumulation by juveniles and pediveligers of the Japanese oyster *Crassostrea gigas* Thunberg. Aquaculture 13:205-212.

Food and Agriculture Organization of the United Nations. 1974. Fish and Shellfish Hygiene. World Health Organization Expert Committee (eds.), Rome, Italy.

Glude, J. B. 1978. Water quality for aquaculture. Commer. Fish Farmer 4:12-31.

Key, D. 1977. Deposit of molluscan shellfish. Min. Agric. Fish. Food, U.K., Lab. Leafl. No. 34, 9 pp.

Loosanoff, V. L. and H. C. Davis. 1963. Rearing of bivalve mollusks. *In:* F. S. Russell (ed.), Advances in Marine Biology, Academic Press, London 1:1-136.

Mann, R. In press. Growth of *Mytilus edulis* in a waste recycling aquaculture system. Aquaculture.

Mann. R. and J. H. Ryther. 1977. Growth of six species of bivalve molluscs in a waste recycling-aquaculture system. Aquaculture 11:231-245.

M.I.T. Marine Industry Collegium. 1977. Closed-cycle aquaculture. Marine Industry Advisory Services, MIT Sea Grant Program, Cambridge, MA 02139. Opportunity Brief #7. 30 pp.

Neilson, B. J., D. S. Haven, F. O. Perkins, R. Morales-Alamo, and M. W. Rhodes. 1978. Bacterial depuration by the American oyster (*Crassostrea virginica*) under controlled conditions. Va. Inst. Mar. Sci. Spec. Sci. Rep. No. 88, Vol. 2, 48 pp.

Office of Fisheries Development, N.M.F.S. 1977. The Molluscan Shellfish Industries and Water Quality: Problems and Opportunities. Gov. Print. Off., Washington, DC.

Pennec, M., D. Prieur, and P. Chardy. 1973. Developpement larvaire de *Mytilus edulis* (L.) en presence d'antibiotiques. Rev. Inter. Oceanogr. Mediterr. 30:115-137.

Price, A. H., C. T. Hess, and C. W. Smith. 1976. Observations of *Crassostrea virginica* cultured in the heated effluent and discharged radionuclides of a nuclear power reactor. Proc. Natl. Shellfish. Assoc. 66:54-68.

Pruder, G. D., E. T. Bolton, and C. E. Epifanio. 1977. Hatchery techniques for a controlled environment molluscan maricultural system. *In:* Proceedings of the Third Meeting of the I.C.E.S. Working Group on Mariculture, Brest, France. Actes Colloq. C.N.E.X.O. 4:347-351.

Public Service Electric and Gas Company. 1977. Integration of thermal and food processing residuals into a system for commercial culture of freshwater shrimp. (Power plant waste heat utilization in aquaculture). Public Service Electric and Gas Company, New Jersey, Vols. 1, 2, and 3.

Shaw, W. N. 1967. Advances in the off-bottom culture of oysters. *In:* Proc. Gulf Caribb. Fish. Inst., 19th Annu. Sess.:108-115.

Sindermann, C. J. 1970. Principal Diseases of Marine Fish and Shellfish. Academic Press, New York.

Zoellner, D. R. 1977. Water Quality and Molluscan Shellfish: An Overview of the Problems and the Nature of Appropriate Federal Laws. Gov. Print. Off., Washington, DC.

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MICROBIOLOGICAL STANDARDS FOR SHELLFISH GROWING WATERS — PAST, PRESENT AND FUTURE UTILIZATION

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You may remember the old folk song about pretty Molly Malone who pushed her wheelbarrow of cockles and mussels through streets broad and narrow selling her wares. At the end of the song Molly dies of a fever. The National Shellfish Sanitation Program (NSSP) has no theme song, but if one were chosen, perhaps it would be "Molly Malone". As is the case in many of the old ballads, Molly was probably a real person, a popular lass in her neighborhood, who died of typhoid fever from eating her contaminated "alive, alive Oh" mussels and cockles. Unfortunately, Molly was not protected by the guidelines of the NSSP, and there was no growing area standard to protect her and her customers from the hazards of polluted shellfish.

This paper does not assert that eating raw shellfish harvested from uncontrolled growing areas is a hazardous pastime, nor does it intend to influence the consuming public against participating in the succulent delight of the raw bar. It does, however, attempt to interpret the NSSP guidelines that pertain to growing area classification with special emphasis on the coliform microbiological standard for "approved" shellfish growing areas.

Statements have been made in public meetings, in official documents, and in the court that the NSSP microbiological standards for shellfish growing waters limit the harvesting of safe shellfish. Considering the methods and technical equipment available to us, this may be true. It is a simple matter to recognize a grossly polluted or clean area, but it is difficult, at best, to establish a line in a river, cove or estuary that will reasonably guarantee that all shellfish below that line will always be safe for consumption.

In regulating the production of safe shellfish, the control agency has two alternatives. The simplest, least expensive and most obvious is a regulation prohibiting the sale of shellfish which have not been retort-processed or otherwise heat-treated to inactivate microbiological pathogens. These processes would not, however, provide protection against toxic chemicals or marine biotoxins. The other alternative, chosen by the founding fathers of the NSSP in 1925 (1), is to maintain sanitary controls which will result in the harvesting and marketing of safe shellfish. Although the NSSP standards and guidelines do *not* prevent the utilization of shellfish resources, they do define the conditions under which safe shellfish can be harvested and marketed. For example, shellfish grown in contaminated areas can be harvested and marketed if they are properly relayed or depurated according to the NSSP guidelines.

Part I of the NSSP Manual of Operations (2) states, "Growing areas may be designated as approved when: (a) the sanitary survey indicates that pathogenic microorganisms, radionuclides and/or harmful industrial wastes do not reach the area in dangerous concentrations." Under the paragraph entitled satisfactory compliance, the manual states, "the area is not so contaminated with fecal material that consumption of the shellfish might be hazardous." Note, at this point, that the manual does not mention viruses or

bacterial pathogens, just "fecal material." The Public Health assumption today, as it was in 1925, is that the presence of viable fecal microorganisms in shellfish waters is a consumer hazard, although it is recognized that small amounts of viable sewage may be present without incurring a hazard. We accept the long standing public health concept, however, that disease organisms may be present if fecal material is detected in shellfish waters.

The problem that must be resolved by a control agency is how much viable fecal material can be tolerated in shellfish waters, or what level or degree of pollution can be tolerated in the growing area without causing illness to the consumer. From the industry viewpoint, the question is how much risk of illness and loss of consumer confidence should industry be prepared to take? The cost of the last big shellfish-borne hepatitis epidemic in the United States in 1973 (3) was astronomical. How many such outbreaks are we prepared to gamble with every year or every 10 years while attempting to modify the standard?

Theoretically, from a conservative public health view, there should be no viable sewage organisms in "approved" growing areas. In the real world, however, this is an impractical goal.

Although the NSSP coliform standard is commonly referred to as the "70 standard," it is actually a two-part standard, each part being equally important to the correct classification of the water mass which is represented by the accumulated data. The NSSP standard (2) is as follows: "The coliform median MPN (most probable number) of the water does not exceed 70/100 ml and not more than 10 percent of samples ordinarily exceed an MPN of 230 per 100 ml for a 5-tube decimal dilution test in those portions of the area most probably exposed to fecal contamination during the most unfavorable hydrographic and pollution conditions." The promulgators of the standard recognized and allowed for the limitation of the multi-tube fermentation test and acknowledged that the test at intervals would report higher values than 70 although not more than 70 coliforms were actually present. Thus, the limitation of the upper 10 percent at an MPN of 230 made allowance for the variability of the method. It is not the intention of this criterion to permit an area that is grossly contaminated 10 percent of the time to be classified as "approved" for shellfish harvesting.

According to the NSSP's present "70 coliform standard" an "approved" station may have 40% of its sample values in the range of 70-230 and 10% of the samples exceeding 230. Therefore, approximately ½ of the samples taken from a routine sampling station in an "approved" growing area can exceed a coliform MPN of 70.

During the 1971 National Shellfish Sanitation Workshop (4), a representative from one of the state shellfish control programs submitted a proposal to the Microbiology Task Force recommending that the "70 coliform standard" be modified to exclude the upper 10 percentile limitations, leaving only the 70 median requirement. If the workshop had accepted this proposal and removed the 230 MPN limitation at the upper 10 percentile, the revised standard would have permitted approved growing areas to be grossly polluted nearly ½ the time. When we take a close look at the standard and the manner in which it can be used, we must seriously consider the possibility that the standard may not be sufficiently restrictive.

The standard as described in the NSSP Manual of Operations not only states the permissible level of viable sewage organisms as determined by the indicator group, but also establishes the conditions for sampling, that is, "during the most unfavorable hydrographic and pollution conditions." This requirement has been misunderstood, ignored, or vigorously enforced by various control agencies for many years. The standard was not intended to cover natural disasters. Its purpose was to assure that the classification of growing areas would be based upon data reflecting the most adverse conditions of tide, weather, runoff, pollution load or other environmental anomalies affecting growing area quality which occur throughout the year.

In reviewing growing area data from national and international sources, it appears that the most common misinterpretation of the standard is the classification of an area as "approved" when a critical investigation reveals that the area should be classified as "conditionally approved" because of intermittent sewage treatment plant failure or other adverse conditions.

Relating a specific level of viable fecal bacteria in a growing area to a specific number of diseases in shellfish consumers is difficult if not impossible to do. If there were a constant ratio between pathogens and indicator organisms in the growing area it could be done. But in the outfall pipe, the ratio between numbers of pathogens and indicator organisms changes with every milliliter of effluent, depending upon such factors as number of carriers or active cases in the population, degree of treatment of sewage, dilution, and other factors. Shellfish from waters containing relatively high levels of viable sewage organisms could be safely consumed if no pathogens were present. Conversely, shellfish harvested from waters containing relatively low numbers of indicator organisms may cause illness in consumers if high numbers of viable pathogens are present in the sewage.

In an effort to strengthen the NSSP and provide federal regulatory support to state shellfish control programs, in 1975 the FDA proposed Shellfish Safety Regulations that included growing area standards. Because of the strong opposition to the proposed regulations, they were not accepted. However, there are local court cases (concerning the standard) which have given legal recognition to the utilization of the standards.

In 1942, following publication of the Raritan Bay Report and the resulting closures of New York waters, the clam diggers went to court requesting that the court rule against the closures. The court ruled (5) as follows: "Petitioner's attack upon the report, which is general in character and points to no errors in hypothesis, calculation or conclusion, in no way lessens the value of the study as a guide. *Petitioner argues that the report fails to show a single contaminated clam taken from the bay. That is an unimpressive criticism. The presence of polluted waters is sufficient. Authorities should not wait until contamination becomes real.* The only point before the court is whether respondents in adopting the resolution and making the order acted arbitrarily, capriciously or unreasonably, which is the charge of the petitioner. Respondents have acted. The law authorized their acts. Their competence is not questioned. They have decided after investigation and careful consideration. In their returns they set forth the sources of information which prompted them to act. I find that these sources are unassailable. On these merits this court approves of the prohibitory action, but if it did not, on the showing herein presented, it would be unwarranted in substituting its judgment for that of the administrative authorities charged with the responsibility."

The following court decision (6) resulted from a similar situation which occurred in 1977 in New York State: "The evidence received at trial discloses that the testing procedures utilized by the Department of Environmental Conservation are derived from these procedures prescribed by the National Shellfish Sanitation Program, Manual of Operations, Part I, Sanitation of Shellfish Growing Area—1965 Revision, published by United States Department of Health, Education, and Welfare, Public Health Service, Division of Environmental Engineering and Food Protection, Shellfish Sanitation Branch (defendants' Exhibit A in evidence). This manual establishes that a condition absolute for the certification and approval of shellfish lands, based upon a sanitation survey of an area, shall be that the median coliform MPN of the water shall be less than 70 per 100 milliliters.

"Comparing these criteria as established by the National Shellfish Sanitation Program with the methods of testing utilized by the department in this instance, I am satisfied that the testing criteria and methodology of sampling comport with such recognized standards contained in defendants' Exhibit A. The frequency of testing, the physical obtaining of water samples, the initial refrigerated storage of the samples, the laboratory testing of the samples and the ultimate analysis of the results all complied with acceptable scientific procedures.

". . . I hold, therefore, that the defendants have fully complied with the provisions of ECL 13-0307; that the testing of water samples utilizing the coliform testing standard was validly undertaken, was directly related to a public health hazard as determined by both Federal and State authorities, and was based upon scientific standards of testing utilizing the coliform testing methodology.

"I further determine that the action of the Commissioner in issuing the orders, effective May 20, 1977, closing the shellfish lands in question, was not arbitrary and capricious, but was based upon a deliberate determination as reflected in the

testing procedures and the intensive analysis undertaken of the waters in question. I find, therefore, based upon all of the evidence adduced at trial, that the orders of the Commissioner had a rational basis for their issuance.

"Based upon all of the foregoing, there exists no basis for my considering any of the additional remedies sought by the plaintiffs in Action No. 2.

"In conclusion, there is no doubt that the action undertaken by the Department of Environmental Conservation will have an adverse economic impact both upon those who are engaged in the shellfish harvesting and upon those who are engaged in ancillary and service industries involving such harvesting. In closing approximately 1,500 acres in the Great South Bay, the Commissioner has brought the total number of acres now closed to shellfish harvesting to approximately 3,100 acres. The dilemma that has been created brings into sharp focus the many problems resulting from the encroachment of an urbanized society upon an industry having a historical significance of over three hundred years in the bay.

"While I have been concerned in determining these actions with the problem of the application of suitable criteria to gauge such encroachment in terms of shellfish lands, the greater issue posed by uncontrolled pollution has not been addressed. In essence, I have been dealing with effects and not causes.

"It is small consolation to a bayman who earns his livelihood by shellfish harvesting to tell him that more precise criteria may allow the opening of lands now closed to harvesting; in fact this may not be the case, regardless of whatever criteria is used, if the Great South Bay continues to be used as the repository for society's waste products..."

In both of these cases, the significance of the standard and the concept that the public health interest is served by controlling the quality of the growing area waters were recognized and supported by the court.

What alternatives are possible to a growing area standard? State agencies could not afford to test, on a statistically valid basis, every lot of shellfish harvested from their waters for bacterial and viral pathogens to certify their safety. At present, we do not even have an acceptable procedure for the detection and enumeration of the most significant pathogen affecting shellfish consumers, the infectious hepatitis virus. It is highly unlikely that there is a state program in existence which could offer safe raw shellfish on the basis of lot by lot certification by sampling for pathogens, nor is it economically feasible to examine thousands of water samples for enteric pathogens on a monthly basis.

The basic concept of the NSSP is to control the safety of shellfish by preventing contamination of their environment, not to determine whether or not shellfish become contaminated after the fact. Certifying shellfish safety by checking for pathogens would not afford the kind of public health protection the American consumer expects from its control agencies.

The FDA has been supporting research at about $300,000 a year since 1974. Our research efforts are directed toward methods and standards development. We utilize the advice and expertise of the Microbiology and Chemistry Task Forces of the NSSP to guide us in our research efforts. Members of these Task Forces represent State and Federal Control Agencies, industry and the academic community. The Food and Drug Administration will continue to seek guidance in its shellfish safety research activities.

The validity of NSSP growing area microbiological standards has been challenged throughout the history of the Program. According to past experience, it is likely that there will be continued efforts to lower standards for "approved" growing areas. Considering the increased stress on our estuaries because of the demand for multiple water uses and the increase in population growth in coastal areas, this is most unfortunate.

The NSSP microbiological standards and criteria for shellfish growing areas, when used in proper context with other classification criteria, provide adequate consumer protection and protect the shellfish industry by maintaining consumer confidence in the product. The "70 standard" is known and respected worldwide as a basic warranty for safe shellfish. It does not prevent utilization of shellfish resources. It establishes part of the criteria for the safe utilization of that resource.

In the future, as in the past, FDA plans to con-

tinue supporting research leading toward improved growing area criteria and standards. We conclude that until new methods and new information justify a change in position, the most effective means of protecting shellfish consumers, and indirectly the shellfish industry, is to continue to classify and control shellfish growing waters according to present NSSP standards and criteria, thereby limiting the level of pollution in approved growing areas. As the court so eloquently stated, the shellfisherman's problem is the encroachment of pollution, not the growing area standard.

LITERATURE CITED

Report of Committee on Sanitary Control of the Shellfish Industry in the United States. Public Health Reports, Supplement No. 53, 1925.

Manual of Operations, Part I, National Shellfish Sanitation Program, 1965.

Portnoy, B. L., Mackowiak, P. A., Caraway, C. T., et al.: Oyster Associated Hepatitis, Failure of Shellfish Certification Programs to Prevent Outbreaks. JAMA, 223: 1065-1068, 1975.

Proceedings, Seventh National Shellfish Sanitation Workshop, DHEW, PHS, 20-22, Oct. 1971, p. 21.

The New York Law Journal, June 27, 1942.

Villani vs. Berle (91 misc. 2nd 603) (Sup. Ct., Suffolk Co. 1977).

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ENVIRONMENTAL STRESS IN OCEANIC BIVALVE MOLLUSC POPULATIONS

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ABSTRACT

Stresses of natural and man-induced origin can and do affect oceanic bivalve populations as well as estuarine species. Human factors include intensive exploitation, with effects that can be demonstrated; and increasing levels of coastal pollution, with effects that we only partially understand. Natural factors, including oxygen depletion, can have severe impacts on oceanic shellfish populations.

Considering man-induced changes, estuarine and coastal pollution has clearly affected species such as soft clams (Mya arenaria) *and hard clams* (Mercenaria mercenaria) *in areas close to human populations, and there is some evidence that pollution can affect oceanic bivalve populations some distance from shore. Ocean dumping plays an important but not exclusive role. Direct evidence is principally in the form of elevated heavy metal levels, and elevated coliform counts in samples from such populations.*

Although it is often difficult to determine whether declines in abundance of marine species are due to natural factors or to intensive exploitation, there is some indication that recent reductions in populations of surf clams off New Jersey may be influenced by fishing as well as by natural phenomena. Survey indices of abundance have declined sharply since 1965, and have recently begun to fall in intensively fished areas off Virginia. A drastic decline in New Jersey populations in 1976-1977 seems, however, to be related to mortalities from natural causes.

Among the natural causes of stress, large-scale natural oceanographic phenomena, possibly influenced by human inputs of nutrient chemicals, can have profound effects on oceanic bivalve populations, as was demonstrated by the development of a large anoxic zone off the New Jersey coast in 1976. Unusual meteorological and hydrographic conditions, combined with an extensive and persistent algal bloom, have besn identified as the cause of the anoxia, which destroyed an estimated 147,000 metric tons of surf clams, 6,600 metric tons of ocean quahogs, and lesser amounts of sea scallops.

Parasitism and disease, clearly demonstrated to affect estuarine and nearshore bivalve molluscs, have not yet been shown to cause mass mortalities in oceanic bivalves, probably because it is difficult to make continuous observations of such

populations. A number of parasites have been described from oceanic molluscs, but they are the type that would usually produce only sublethal effects on the host.

Thus it seems that stress from natural as well as human perturbations of the environment can affect survival and abundance of oceanic bivalves. Evidence is still scanty, but is increasing concomitantly with closer scrutiny of these species.

INTRODUCTION

The environment of offshore oceanic bivalve molluscs, surf clams (*Spisula solidissima*), ocean quahogs (*Arctica islandica*) and sea scallops (*Placopecten magellanicus*), would seem superficially to be a reasonably tranquil one, free from many of the drastic perturbations that characterize the estuarine and littoral zones. There is recent evidence, however, that the ordered existence of these species can be disturbed, sometimes drastically, by natural and man-induced changes in the chemical, physical, and biological environment. These changes produce stress on individuals and populations, and may in the extreme result in mass mortalities.

The oceanic bivalves are usually seen from the human perspective of resource species, to be harvested, managed, and eventually cultured. Such populations might be considered from another perspective — that of the animals themselves, as part of the benthic ecosystem, ensconced in or on the sea bottom, dimly sensing what should be for them a reasonably stable environment, unaware of, and probably not too much concerned about, the human species in a foreign environment above them. In this benthic environment, population density is controlled, food supply and oxygen are provided, temperature and salinity ars stable, predator pressure on adults is minimal; all of this should lead to a reasonably placid existence.

There are, however, natural and man-made pressures on oceanic bivalve populations that are not always apparent, but that may affect population size. Natural pressures may take the form of predation, competition, disease, inadequate food, and marginal or lethal physical/chemical environmental conditions, such as abnormal temperatures or inadequate dissolved oxygen in bottom waters. Human pressures on oceanic bivalves include effects of pollution and intensive exploitation.

This paper summarizes some of the available information about effects of representative categories of environmental stressors, natural and man-induced, on oceanic bivalve populations. It is not intended as a review, but is instead designed to emphasize the effects of selected environmental factors on survival and well-being of the deeper-water bivalves, which often escape the direct scrutiny possible with estuarine or nearshore species.

EFFECTS OF HUMAN ACTIVITIES ON OCEANIC BIVALVES

Oceanic bivalves normally occur at depths where they have escaped the intensive scrutiny, manipulation, and harvest by humans that characterize intertidal or shallow subtidal species such as oysters and mussels. Within the past several decades, however, two human activities, intensive mechanized fishing and coastal pollution, have begun to affect offshore populations. Effects of both activities are beginning to be documented in the scientific literature, although the evidence to date could not be described as overwhelming.

Effects of Ocean Pollution

It is apparent that human chemical additions have introduced or have increased environmental stresses for shellfish in estuarine and coastal waters. We have, for instance, added pesticides and other synthetic chemicals which can, even in low concentrations, drastically affect the physiology of fish and shellfish, and with which the species may have had no previous evolutionary experience. We have added heavy organic loads, in the form of sewage sludge and effluents, which can produce anaerobic or low-oxygen environments, and which are often accompanied by other contaminants such as heavy metals, that can interfere with enzymes of the shellfish and the food organisms they consume.

It is also apparent that there has been a gradual

increase in amounts of polluted coastal/estuarine areas, an increase that is generally proportional to the density of the adjacent human population and its level of industrialization. We have excellent documented examples of this in North America.

Humans have now begun to impinge on the existence of oceanic bivalves, as they so long ago impinged upon populations of estuarine and nearshore bivalves. The process has only started, but there are disquieting signs of disturbance, of developing stress, in such populations.

Pollution of offshore shellfish growing areas by ocean disposal of wastes — ocean dumping — is an existing problem. The taking of shellfish is now prohibited in zones around the New York and Philadelphia ocean dump sites (Figure 1), because of demonstrated microbial and heavy metal contamination. Heavy metals well above background levels have been found in surf clams from both dump site areas, for example, and a recent report (Wenzloff et al., 1979) points out other interesting events concerned with heavy metal pollution in the Middle Atlantic Bight:

1. Higher heavy metal levels (especially lead and cadmium) were found in ocean quahogs than in surf clams.

2. Highest levels of several metals in both species were found in the New York area, with decreasing values toward Cape Hatteras (a four-to-five-fold decrease in silver, zinc, arsenic, copper, cadmium, and chromium). Mercury was below detection limits in most samples.

3. Some anomalies (higher values) were found in the vicinity of the Philadelphia sludge dump site and the Dupont acid waste site (Figure 1).

4. No levels were high enough to be considered a threat to public health, in that they were below action levels set by other countries (the Food and Drug Administration (FDA) has set no action levels for the United States, except for mercury).

We have not yet seen, to my knowledge, any significant direct effect of ocean dumping on abundance of offshore molluscan resources. Effects thus far concern lack of access to the resources in the impacted areas (closed to harvesting); and a vague uneasiness about possible public health problems in peripheral areas, and about sublethal effects of pollutant chemicals on the molluscs.

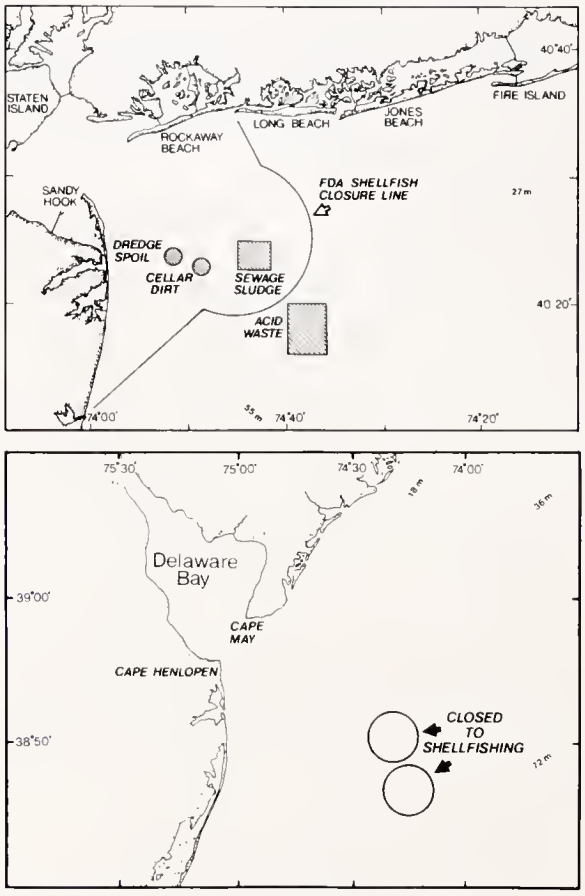

FIGURE 1. *Dump site and dump-site areas closed to shellfishing.*

The problem of contamination of oceanic shellfish beds is not a simple one, as was pointed out in a recent impact analysis of effects of ocean dumping off the Maryland coast (the so-called Philadelphia dump site) by Forste and Rinaldo (1977). Closure of an area by FDA of course results in removal of shellfish in that area from exploitation (an estimated 600,000 bushels of ocean quahogs in the closed area off Maryland, for example), but there are subsidiary effects as well:

1. *Expansion of contaminated zones.*

Fecal coliform levels were high as far as 11 miles from the closed area off Maryland, according to Forste and Rinaldo. Such findings raise the possibility of additional closures.

2. *Spread of the sludge plume.*

Prevailing current patterns and continued dumping can result in deposition of organic

sediments far beyond actual dump site areas. The Philadelphia sludge dump site plume, for example, was depicted by Forste and Rinaldo to extend well south of the closed area. However, no effects on abundance of shellfish have been demonstrated in this plume area.

3. *Possible oxygen depletion resulting from organic loading.*

Addition of substantial amounts of oxygen-demanding organic wastes to continental shelf areas may lead to at least localized oxygen depletion in bottom waters, particularly if dissolved oxygen levels are marginal for survival of benthic animals under existing natural conditions. As yet, however, no clear relationship of mass mortalities of shellfish with oxygen depletion caused by sludge dumping has been demonstrated.

4. *Contamination of shellfish beds by "short dumping."*

Sludge dumping outside designated dump sites has been documented on several occasions. Such short dumping can contaminate oceanic shellfish beds wherever it occurs. This is obviously an enforcement problem, but a difficult one to deal with effectively.

5. *Possible long-term effects on abundance.*

There is a large body of published experimental data on acute effects of chemical contaminants (heavy metals, halogenated hydrocarbons, and petroleum components) on life history stages of marine animals. Localized effects of acute contamination by oil spills on estuarine/coastal shellfish beds have been documented (see for example Dow, 1975), but evidence does not exist for comparable acute effects of pollutants on abundance of offshore species such as those of concern to this paper. Long-term effects of contaminants on survival of life stages of shellfish have also been demonstrated experimentally, but application of findings to natural populations must be made with great care and conservatism, particularly when dealing with deeper-water species.

Thus there are several direct and potential impacts of ocean dumping on oceanic shellfish harvesting. Economic impacts of closures can be estimated, but biological impacts on abundance of commercial shellfish have yet to be determined, and will be very difficult to determine until we have better understanding of the natural factors that affect population abundance.

Effects of Exploitation

Abundance of surf clams and other oceanic bivalves has clearly been affected by another of man's activities — fishing. Predation by humans, using increasingly efficient devices, can exert significant stress on existing populations; this has been demonstrated in the surf clam fishery, which has progressed from the inefficient dry dredge of the 1940's to the ever larger stern mounted hydraulic dredges of the 1970's. Landings of surf clams increased during the period 1955 to 1974 from 5,000 metric tons to 48,000 metric tons (1974), then dropped to about 25,000 MT in 1976 and 1977 (Figure 2).

Ocean quahog landings in the period 1955 to 1968 were only about 50 to 100 MT, which increased to 500 MT from 1969 to 1975, and then in 1976 to 2,850 MT and in 1977 to 8,250 MT. This species is presently underutilized, but its reported very slow growth rate may require early imposition of limits on total catches if sustained production is to be realized.

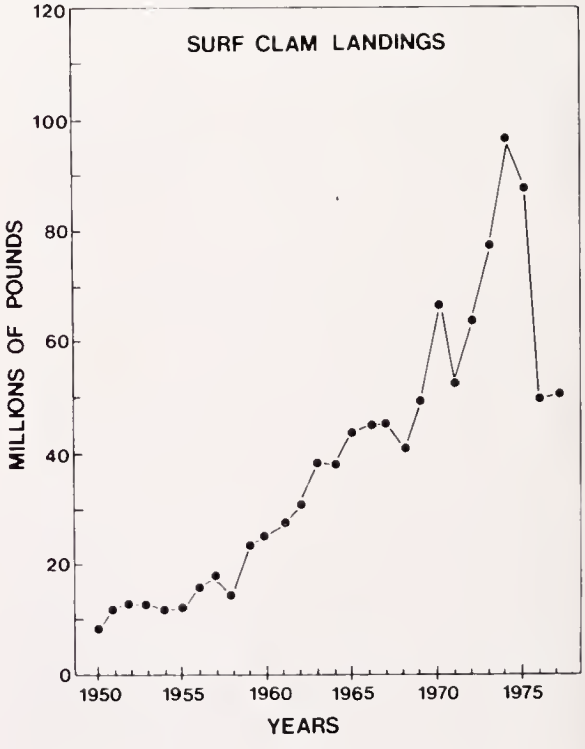

FIGURE 2. *Surf clam landings, 1950-1977.*

Landings of sea scallops by U. S. fishermen were low from 1969 to 1974 (about 3,000 MT), then increased to over 8,000 MT in 1976, due to recruitment of the strong 1972 year class — the first good year class in a number of years.

Catches of surf clams and survey indices of abundance have declined during the past decade in New Jersey waters, where much of the surf clam industry was centered during the 1950's and early 1960's. Newly discovered beds off Virginia were then fished intensively, and survey indices and catches there have also begun to fall.

New Jersey surf clam statistics since 1965 illustrate the concomitant decline in survey indices and catches:

1965-1967 survey indices averaged 43 clams/tow and catches averaged 15,000 MT.

1969-1970 survey indices averaged 26 clams/tow and catches averaged 7,500 MT.

1976-1977 survey indices averaged only 7.8 clams/tow with estimated catches between 2,000-2,700 MT (Murawsky, 1977).

Because of the sedentary nature of oceanic bivalves, they are particularly vulnerable to intensive highly mechanized fisheries. The need for stock management, particularly for slow growing species, is very real. Since all the species of concern to this paper have a history of only sporadic successful sets, management problems are intensified. Furthermore, species such as the surf clam set successfully in some areas and not others in any given year, and the intensity of setting varies from year to year.

EFFECTS OF NATURAL STRESSORS ON OCEANIC BIVALVES

From the preceding sections, it is apparent that man-made pressures on oceanic bivalves exist, and seem to be increasing. However, the pressures must be seen and evaluated against a background of natural environmental pressures and events which can affect survival; these are pressures with which the species has always had to contend. Included would be extreme departures from normal conditions of temperature, salinity, currents, and dissolved oxygen, unusual abundance of predators, disease outbreaks, or extreme scarcity of food (particularly during larval stages). There is some recent information about two of these limiting influences on population abundance — oxygen deficiency and parasitic disease — and these will be the focus of this section.

Effects of Oxygen Depletion

A textbook example of a large-scale environmental event took place on the continental shelf of the Middle Atlantic states in 1976. An anoxic water mass, which destroyed much of the surf clam stocks off central New Jersey and affected other species, developed in the summer and early autumn of that year. This extreme oxygen depletion was considered to be driven principally by natural mechanisms, but was undoubtedly augmented by human organic additions to coastal waters.

Our involvement in this event began with reports during the first week of July, 1976, from sport divers, lobstermen, and trawler fishermen, of dead and dying animals of all kinds on fishing reefs and wrecks off the coast.

At first we were only moderately interested, since similar very localized events had occurred in 1968, 1971, and 1974. Within a few days, how-

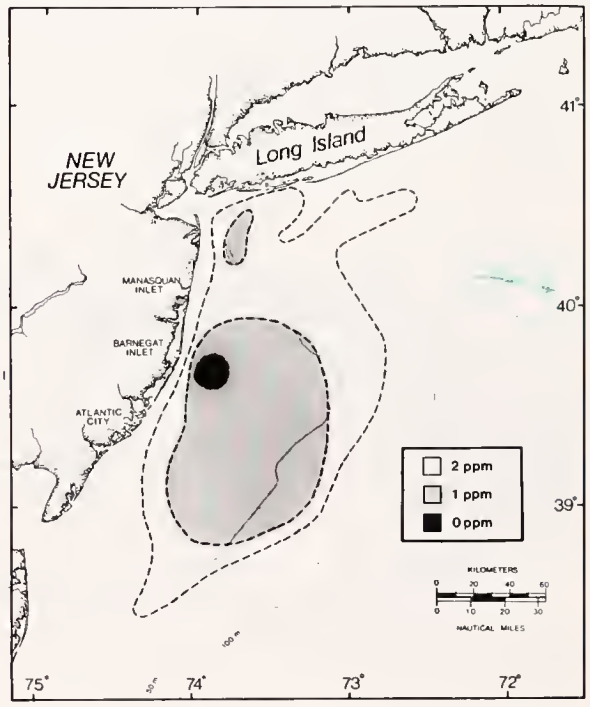

FIGURE 3. *Maximum extent of oxygen-depleted water on the U. S. Atlantic continental shelf in 1976.*

ever, the reported mortality areas had extended southward some 70 km and well out on the continental shelf. We began a series of survey cruises to assess the damage — cruises which had to be expanded further and further southward, all the way to Delaware Bay, and seaward for 85 km. Oxygen deficient bottom water — sometimes with zero dissolved oxygen levels, was found in a zone with a coastal distance of some 165 km, in a corridor from 5 to 85 km off the coast (Figure 3). We knew then that we were in the presence of an environmental event of epic proportions.

In the central coastal area oxygen values below the thermocline were zero, and hydrogen sulfide was formed. The anoxic condition persisted until October, when lower surface temperatures and mixing after disappearance of the thermocline gradually reoxygenated the bottom water.

Mortalities of fish, lobsters, and molluscan shellfish were observed. The sedentary forms — surf clams, ocean quahogs, sea scallops, and the benthic infauna — suffered the greatest mortalities. From our weekly surveys during the anoxic episode we estimated that at least 16% of the surf clam population off the Middle Atlantic coast — some 147,000 tons, had been destroyed by October (Figure 4), with significant but lesser mortalities of ocean quahogs and sea scallops. Lobster catches were reduced by almost 50% during the period.

As might be expected, the man in the street and the newspaper headline writers immediately jumped to the conclusion that ocean disposal of pollutants, particularly sewage sludge dumping which goes on at a grand scale 15 km from the coast, was responsible for this environmental catastrophe.

FIGURE 4. *Surf clam dredge collection, August, 1976. Note empty shells and decaying meats. (Photograph courtesy of John Ropes, Woods Hole Laboratory, NEFC, NMFS).*

Our studies suggested that large-scale meteorological and oceanographic phenomena were involved in production of the extensive anoxic zone which resulted in mortalities. A large amount of data has been assembled and a hypothesis developed, centering on a combination of anomalous environmental events superimposed on a marginal coastal area, which has been made eutrophic by man's inputs of organic material.

Meteorological events included:

High February-March temperatures with peak river runoff in February instead of April.

Reduction of cyclonic storm activity during the summer to less than half the 25-year average.

A period of 4-6 weeks in June-July with persistent and abnormal south or southwest winds.

Physical events included:

Early (February-March) warming of surface

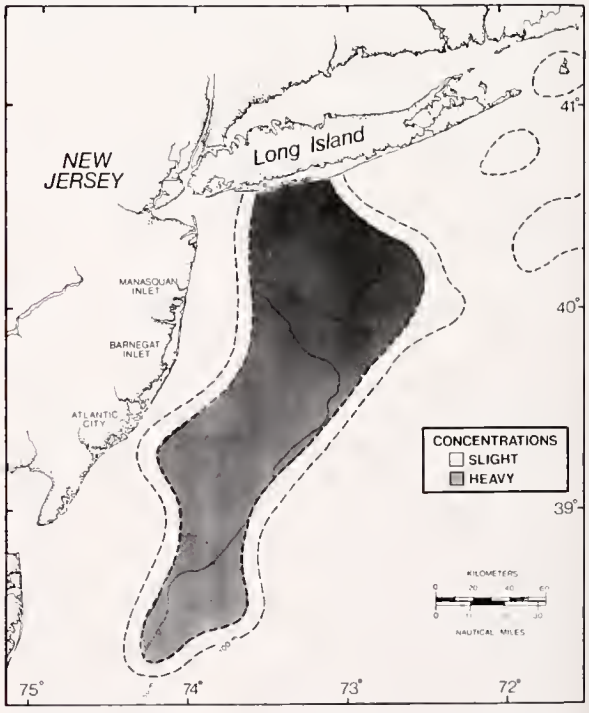

FIGURE 5. *Extent of* Ceratium tripos *bloom, March, 1976.*

waters and early development of the thermocline.

Reduction in velocity and even reversal in direction of the normal southward drift of shelf water.

Biological events included:

A massive bloom of the dinoflagellate *Ceratium trios* over much of the Middle Atlantic Bight, but particularly concentrated in the New York Bight (Figure 5). The bloom began in February and persisted at least until July, and was concentrated at and just below the thermocline.

So, if oxygen demand from a declining phytoplankton bloom is superimposed on an area (the New York Bight) already characterized by reduced dissolved oxygen in an average summer; and if this organically rich oxygen demanding water is sealed off early in spring by the early onset of a thermocline; and if water mass movement is reduced to a minimum flow of bottom water, the ingredients of disaster to marine animals are present.

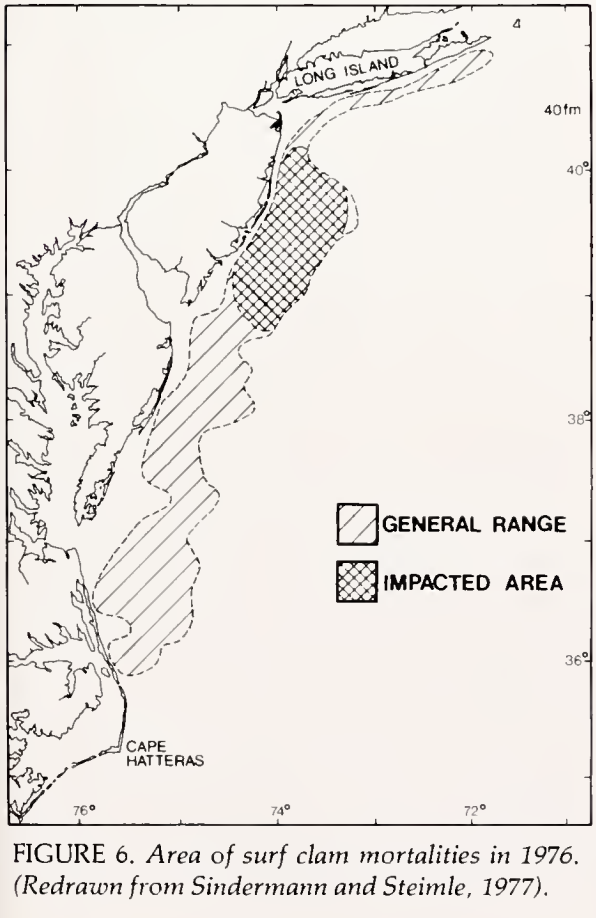

FIGURE 6. *Area of surf clam mortalities in 1976. (Redrawn from Sindermann and Steimle, 1977).*

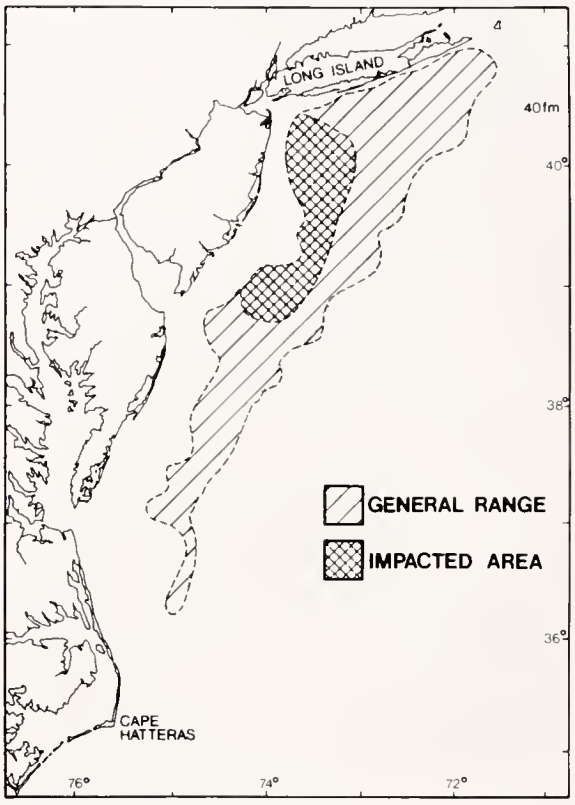

FIGURE 7. *Area of ocean quahog mortalities in 1976. (Redrawn from Sindermann and Steimle, 1977).*

Specific population impacts were rather precisely determined: Effects of anoxia on surf clams *(Spisula solidissima)* were most severe. The biomass loss was 85% within the impact zone — an estimated 147,000 MT of meats or 16% of the estimated total surf clam population of the Middle Atlantic Bight. The area of maximum mortality was 6,700 km² in a corridor along the shelf (Figure 6), to a depth of 36 meters; but a narrow coastal zone, from 5 to 15 km from shore was less affected.

Effects of anoxia on ocean quahogs *(Arctica islandica)* were less dramatic, since the main concentration of the resource is seaward of 36 m depth and only the shoreward margins were affected. The affected area covered 9,150 km², and 25% of the population in the marginal area was destroyed (Figure 7). This represents less than 1% of the estimated total Middle Atlantic stocks.

Effects of anoxia on sea scallops *(Placopecten*

magellanicus) were also less dramatic since the principal resource is also seaward of 36 m depth, and only the shoreward margins were affected. Mortalities of 9-13% were found in a 4,300 km² area (Figure 8).

When confronted as we were with such a resource catastrophe, many difficult questions came crowding in:

"Have such anoxic events occurred in that area before?" Yes, in 1968, 1971, and 1974 to a *much* smaller degree, based on very limited information, and perhaps at other times and in other surf clam areas, where sudden and unexplained reductions in abundance have been seen.

Another question has been *"What is the recovery rate of a species such as the surf clam in an area where the population has been largely destroyed?"* The adult clam population of the totally anoxic area was virtually eliminated. There was little evidence of survival of the 1976 year class which may have set in the impacted zone, but spatfall in 1977 from larvae produced outside the mortality zone was good. (Survival of the 1977 year class in 1978 was poor, however). We plan to examine the repopulation process annually, since this can be treated as a massive field experiment.

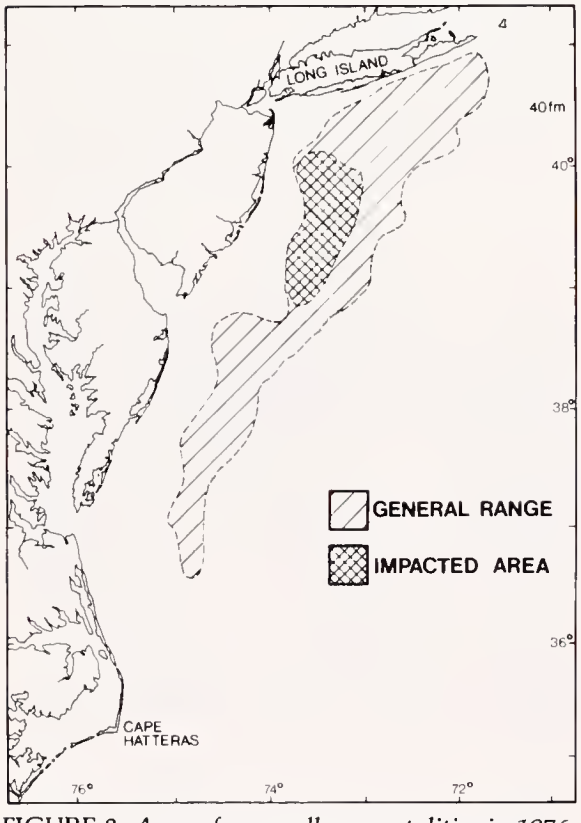

FIGURE 8. *Area of sea scallop mortalities in 1976. (Redrawn from Sindermann and Steimle, 1977).*

A more difficult question is *"What is the relative importance of man-made intrusions?"* Human organic contributions to New York Bight waters are substantial. An estimated 130 tons of nitrogen is supplied from the Hudson River estuarine system per day, and sludge dumping 15 km off the coast supplies another 20 tons per day in a concentrated area. The background mass load of nitrogen from the outer oceanic boundary of the Bight is unknown (although estimates have been made), but in a marginal environment, any addition to the total mass load may be harmful. Human sources are thought to contribute less than 10% (and possibly only about 2%) of the total mass load of nitrogen in the New York Bight.

Another question is *"Will this event happen again?"* It seems quite possible. In 1977, oxygen sagged badly in a zone 5-20 km off the coast of New Jersey in August, but then stabilized in late August. No stressed animals or mortalities were reported. In 1978, two moderate phytoplankton blooms were reported off the coast, *Coscinodiscus* (a diatom) in March-April and *Ceratium* in June and July, but the late onset of the thermocline in 1978 may have prevented total depletion. Oxygen values sagged badly in August and early September in the same coastal band as in 1977, but did not reach zero. Scattered reports of abnormal fish on submerged wrecks and reefs were received in September, but no mass mortalities were seen. It seems that the entire coastal sector is very marginal, and may be pushed over the edge into anoxia in any year, with the right combination of physical, biological, and chemical ingredients.

A final question is: *"Have similar mass mortalities due to natural physical or chemical environmental extremes occurred elsewhere in oceanic bivalve populations?"*

The intuitive answer would be "probably" — and there is some limited evidence. Probably the best comes from the Canadian literature on sea scallop mortalities in the Gulf of Saint Lawrence, where in 9 of 33 years from 1928 to 1961 there were extensive midsummer mass scallop mor-

talities due apparently to sudden increases in bottom water temperatures in the southern Gulf, caused by wind-induced oscillations of the thermocline (Dickie and Medcof, 1963; Medcof and Bourne, 1964). Water temperatures apparently exceeded the upper incipient lethal temperature for scallops, and mortalities of up to 80% were observed (normal annual mortality has been estimated at 10%).

There were many similarities between the Canadian scallop mortalities and the anoxia effects on surf clams in the Middle Atlantic Bight; the principal one being the presence of a marginal environment, subject to hydrographic perturbations which exceeded the limits of tolerance of the dominant oceanic bivalve for a long enough period to produce mass mortalities.

Effects of Parasitism and Disease

Biological stressors can also include parasitism and disease, which can kill or weaken individuals. We have as yet no substantiated reports of epizootics and resultant mass mortalities in oceanic bivalves similar to those that have been reported in oysters. This may well be because most of these populations are beyond the range of close scrutiny.

Recently, however, several parasites of oceanic bivalves have received attention. The first is a larval nematode, *Sulcascaris sulcata*, which occurs in surf clams and calico scallops. In clams, up to 78% of individuals in samples from Virginia were found infected (Kern, 1977) with an overall prevalence of 32%. Infestations were much lower in New Jersey and Maryland. High prevalences of the same nematode were seen earlier in the adductor muscles of calico scallops (Sindermann, unpublished data). The worm, a larval ascaridoid, is usually enclosed in a brownish cyst. It is normally found in the visceral mass of the clam, but can be found in any tissues. The definitive hosts, identified recently by Lichtenfels et al. (1978) are marine turtles (loggerhead and green) so the worm does not seem to present a public health problem; but it may present a problem for the clam and scallop host, because of debilitation resulting from migrations of the larval worms through the tissues.

Another larval worm in surf clams is undoubtedly more important from the clam's point of view, because it destroys the gonad of the host. This is an unidentified larval trematode, which proliferates in the gonad and digestive gland, eventually completely destroying the gonad and eliminating the animal as a reproductive part of the population. Fortunately, the reported occurrence of this parasite is low in surf clam populations — well under 1% in samples examined by John Ropes of the Woods Hole Laboratory, National Marine Fisheries Service, who first observed the presence of the worm, and has examined many histological sections to determine its abundance (Ropes, J., personal communication).

A few other parasites of offshore molluscs are known: Ropes and Merrill (1967) described a nemertean worm from the mantle cavity of offshore hard clams *(Mercenaria campechienses)*; Medcof (1949) described a shell-destroying sponge from sea scallops; and parasitic pyramidellid snails cause shell and mantle abnormalities in sea scallops (Merrill and Boss, 1964). While these parasites are not known to cause mortality, they all obviously have sublethal deleterious effects on their hosts.

DISCUSSION

It seems almost unfair to isolate and discuss only a few of the many environmental factors, physical, chemical, and biological, that can affect survival of offshore bivalve molluscs. The full slate of possible candidates for discussion is illustrated in Figure 9; from this array of factors only four: pollution, human predation, oxygen deficient bottom water, and disease, have been con-

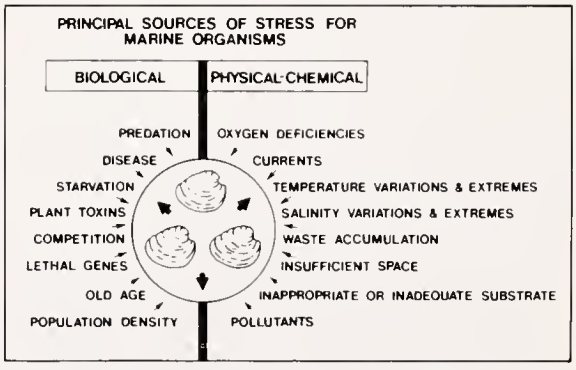

FIGURE 9. *Principal sources of environmental stress for marine animals.*

sidered in this paper. However, these examples can serve to make the point that some information is available about how environmental stresses affect offshore bivalves. The evidence is not massive, but it is accumulating, and it does point to a number of generalizations:

(1) Mass mortalities can result from extremes of environmental perturbations, beyond the physiological limits of the species involved.

(2) Probably as important as mass mortalities are the less obvious or "background" mortalities, which extract individuals from the population gradually, or render individuals more susceptible to other environmental stresses.

(3) The so-called "resiliency" of marine populations is highly variable, since some mass mortalities are followed by very slow recovery of affected populations, while in other instances populations rebound rapidly. The amplitude of population fluctuations can be significantly affected by stresses which result in mass mortalities.

(4) Success of reproduction and survival of year classes depend on the persistence of a dynamic, even precarious, equilibrium, and man in some instances seems to be disturbing that equilibrium, by imposing additional environmental stresses.

(5) Despite greater emphasis on marine studies, we are still often unable to distinguish with certainty between natural and man-made impacts on resource species.

(6) At least some of the catastrophic events that have been described may have paleontological significance — because of the sheer numbers and the great areas involved, because environmental conditions could favor preservation, and because some events are repeated.

The research task of course is to understand and evaluate the effects of *all* the environmental stresses, natural and man-induced, on population abundance, and to offer advice on management of stocks that will take these factors into account.

LITERATURE CITED

Dickie, L. M. and J. C. Medcof. 1963. Causes of mass mortalities of scallops *(Placopecten magellanicus)* in the southwestern Gulf of Saint Lawrence. J. Fish. Res. Bd. Can, 20: 451-482.

Dow, R. L. 1975. Reduced growth and survival of clams transplanted to an oil spill site. Mar. Poll. Bull. 6: 124-125.

Forste, R. H. and R. G. Rinaldo. 1977. Estimated impacts of the Philadelphia dump site on the sea clam fishery. Md. Dept. Nat. Resources, Doc. FA-MRR-77-1, 22 pp.

Kern, F. G. III. 1977. Distribution and prevalence of larval anisakid nematodes in surf clams from the Middle Atlantic coast. (Abstract) Pgm. and Abs. 52nd Annual Mtg. Am. Soc. Parasitol. 14-19 Aug. 1977, Las Vegas, Nev., p. 53.

Lichtenfels, J. R., J. W. Bier, P. A. Madden. 1978. Larval anisakid *(Sulcascaris)* nematodes from Atlantic molluscs with marine turtles as definitive hosts. Trans. Am. Mic. Soc. 97: 199-207.

Medcof, J. C. and N. Bourne. 1964. Causes of mortality of the sea scallop, *Placopecten magellanicus*. Proc. Nat. Shellf. Assoc. 45: 184-186.

Medcof, J. C. 1949. Dark meat and the shell disease of scallops. Fish. Res. Bd. Can., Prog. Repts. Atl. Coast Sta. No. 45, pp. 3-6.

Merrill, A. S. and K. J. Boss. 1964. Reactions of hosts to proboscis penetration by *Odostomia seminuda* (Pyramidellidae). Nautilus 78: 42-45.

Murawski, S. A. 1977. Evaluation of losses of surf clams, *Spisula solidissima*, and ocean quahogs, *Arctica islandica*, due to oxygen depletion off the New Jersey coast during 1976. Northeast Fisheries Center, NMFS, Woods Hole Laboratory Report (unpublished), 32 pp.

Sindermann, C. J. and F. W. Steimle. 1977. Oxygen depletion and mass mortalities of shellfish in the Middle Atlantic Bight of the United States in 1976. Internat. Counc. Expl. Sea, Doc. CM1977/E:13, 27 pp.

Ropes, J. W. and A. S. Merrill. 1967. *Malacobdella grossa* in *Pitar morrhuana* and *Mercenaria campechiensis*. Nautilus 81: 37-40.

Wenzloff, D. R., R. A. Greig, A. S. Merrill and J. W. Ropes, 1979. A survey of heavy metals in two bivalve molluscs of the mid-Atlantic coast of the United States. Fish. Bull. 77:280-285.

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FOOD SCIENCE — INCREASING DEMAND FOR SHELLFISH PRODUCTS

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At the National Blue Crab Industry Workshop in Charleston, SC, last year, Mr. George Harrison, Jr., gave a presentation which included the following:

"In 1902, my grandfather put crabs into a basket, dropped them into a retort and cooked them; took them out, and cooled them off. He took out his trusty knife, picked the meat, packed the crabmeat in oyster cans, iced the cans in a wooden box, and put them on a steamboat to be shipped to market. In 1977, if not fully rusted away, somebody is still using that retort. The cans today are made of lighter alloys but are basically the same. And if that old wooden fish box could be found and somebody could repair it, it would still be in use. The knives are mechanically ground, and the wooden handle is gone, and the steamboat has given way to the truck. Last, but not least, the same fish market is still receiving crabmeat from all of us. In short, the past 75 years have given us little progress. The blue crab industry today is where the bulk of the U.S. Food Industry was 50 years ago."

Although these statements concern the blue crab industry, the same things could be said of much of the shellfish industry in the U.S. The oyster industry represents another example. At one time, oysters were considered a common food. It is said that in the late 1800's, New York City alone consumed more oysters than our present entire annual catch. In 1890-1892, the total U.S. production was about 183 million pounds of meats annually compared to about 54 million pounds during the 1970's. With the exception of a few large commercial operations, the industry has remained virtually unchanged. Meat processing facilities are small, labor intensive and marginally profitable. And for the most part, the marketing of oysters is still limited to shell stock, fresh shucked meats and canned oysters. Even if the resource base is improved substantially through aquaculture and pollution abatement, I personally feel that neither the processing sector nor the present markets can absorb the increase in volume without major advances in processing technology, and new market development.

The shellfish processor is presently faced with increasing operating costs, lack of available labor, competition in the market place, and ever increasing interference through government regulations. These factors are forcing the industry to become more efficient in their operations, and they must look to new technology for automation, new packaging techniques, and new product development.

Over the past two or three years, there have been some interesting developments in food science and engineering which could have a major impact on the shellfish industry. One of these is called "reforming" or "restructuring," where small particles of meats can be formed into attractive products using binding agents.

One process that is presently being used in the shellfish industry is an extrusion system using a calcium alginate binder. This process involves mixing a minced seafood product such as clam

meats or shrimp with sodium alginate, a natural product from seaweed. A shaped product such as a strip or a ring is formed by means of an extruder. After forming, the product is immersed in a calcium ion solution usually calcium chloride. The calcium ions replace the sodium ions of the alginate and produce a gel skin which solidifies the shape of the product for battering and breading by conventional machines.

Since these alginate gels are stable during freezing and thawing and also heat processing, many other applications are possible. At the Gloucester Laboratory, we have been working with alginate systems with crabmeat. However, in our work we are attempting to produce a uniform texture throughout the product in order to resemble the typical flaky texture normally perceived in crabmeat. In our process, we prepare a mixture of 3 parts crabmeat to 1 part sodium alginate. We then form a lump and hold shape by spraying with 5 percent $CaCl_2$. The product is then soaked for 40 minutes in 5 percent $CaCl_2$ to form a gel throughout the product. The resulting product has the appearance, flavor, and texture of a crabmeat lump which can be frozen, pasteurized, or sterilized.

This process is somewhat lengthy for commercial production; however, there is the possibility of using an extrusion technique. So far, all our work in this area has been done on minced fish flesh, but there is no reason why the concept should not work with crabmeat or other shellfish.

Using a forming machine, we continuously extrude thin sheets of flesh, each of which are coated with the required amount of sodium alginate and calcium solution to form a gel. We then layer the sheets to produce a multilayered block. If we then cut or stamp out pieces across the grain, we can produce a product that simulates flakiness. Taste test results using minced flesh indicate a very high acceptability comparing this product to natural fillet products.

We have also developed a system for producing crabmeat lumps or pieces where no additives are necessary to bind the product. In this case, we use a new system of crabmeat picking called "roller extraction". The basic concept of the roller extraction machine is shown in the schematic in Figure 1 and the prototype unit used in the laboratory is

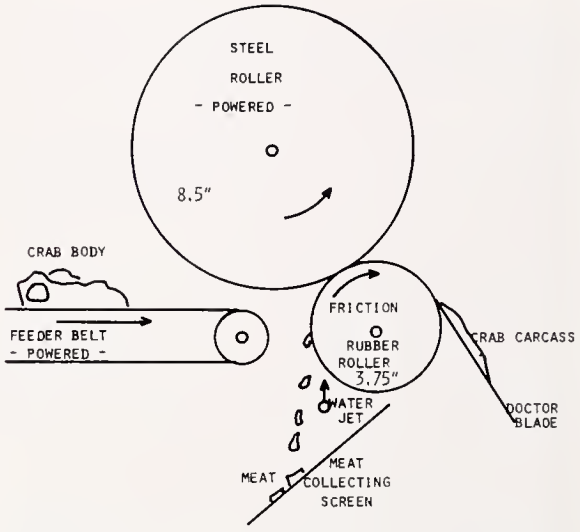

FIGURE 1. *Cross section schematic of roller table used for the extraction of crabmeat.*

shown in Figure 2. This type of machine processing requires a two-stage cooking process which has been proven acceptable for blue crab, red crab, and snow crab processing. Typically, the crab section or body is first blanched in hot water (60-70C) to partly solidify the meat and free it from the shell. At this point, the meat is semi-raw and somewhat gelatinous. This allows the meat to be squeezed from the shell by the rollers without rupturing the internal cartilage material producing a shell-free meat. After the extraction process, the meats are cooked in steam (100C) to produce the final cooked crabmeat product. This process produces a flake meat which is highly acceptable but by no means can compete with lumpmeat in the market place. However, since the crabmeat is semi-raw after extraction and the proteins still have binding capacity, lumps or pieces can be formed and cooked into solid lumps or portions. Organoleptic evaluations in the laboratory have shown that in common crabmeat recipes comparing reformed blue crabmeat lumps to commercially handpicked lumpmeat there was no significant difference in overall quality. The reformed lumpmeat, however, had a much longer fresh shelf life (18 days) and retained quality longer during frozen storage.

Another way to approach a technological problem is to find a successful processing method and adapt it to a new use. Over the last several years,

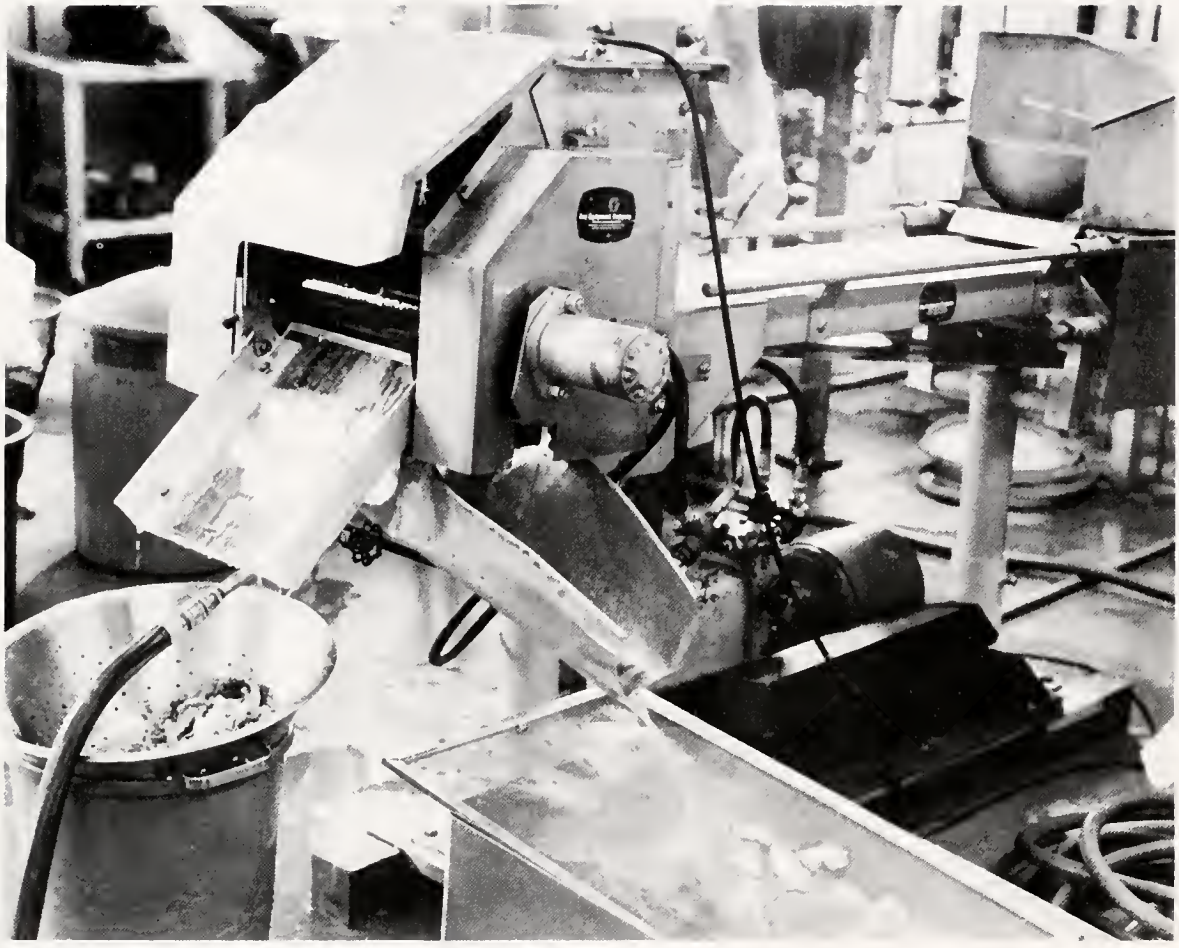

FIGURE 2. *Roller extraction machine for crabmeat.*

we have attempted to develop new product concepts for frozen oysters. The problems which always have confronted us were the physiological limitations of the raw oyster meat and the unavailability of machine processing.

There are many problems associated with freezing oyster meats. During frozen storage there are marked changes in flavor and texture, drip loss increases, and the oyster meats have a tendency to discolor. During our research on the freezing of oysters, a suggestion was made by Mr. Gordon Hallock from the State of Maryland Seafood Marketing Authority and Mr. Robert Prier of the Cheasapeake Bay Seafood Industries Association that frozen "heat n serve" oyster products might be prepared using cooked or blanched oysters as a raw material. Since the "steam and shake" method of shucking oysters represents the only automated procedure used in the industry, this seemed to be a very reasonable approach to the problem.

The primary area of our investigation was to determine the potential of steam-removed cooked oyster meats as an acceptable frozen food item by: 1) determining cooking methods consistent with optimum meat yield, 2) obtaining data on the refrigerated and frozen shelf life of cooked oyster meats, 3) developing means for suppressing oxidative rancidity in frozen oyster packs, and 4) developing new product forms from these cooked meats.

Preliminary tests on frozen oyster meats yielded some very encouraging results in terms of developing frozen cooked oyster products. The frozen samples of cooked meats appeared far

superior to raw frozen meats. These oysters retained the characteristic flavor of an oyster, and wateriness and discoloration were not problems. However, we did have some problems where after two or three months of frozen storage; the cooked oyster meats became rancid.

A series of tests were run to develop a method of suppressing the development of rancidity during frozen storage. Cooked oysters were treated with common antioxidants; the meats were frozen and then tested for quality after three and six months. The series of tests using a 1 percent ascorbic acid dip treatment indicated that this procedure resulted in acceptable quality meats after six months frozen storage as determined by TBA values and organoleptic tests.

One of the most important segments of our work was to develop new frozen products using cooked oyster meats as the raw material. These were items which could be frozen in bulk for reprocessing and also marketed as frozen prepared products to be used directly by the consumer.

Products tested were steamed out meats frozen into blocks, breaded oyster sticks, oysters frozen in bulk in their own nectar, and oysters frozen in cocktail sauce similar to the present shrimp cocktail products. In general, these products when treated with ascorbic acid to reduce rancidity were acceptable through several months of frozen storage. Oysters frozen in cocktail sauce remained acceptable for over a year.

Two semicommercial tests were carried out during the study. In one test, 100 bushels of oysters were steamed and the meats removed by hand. The cooked meats were washed and packed in gallons and shipped to Boston fresh in ice. Three days later, the oysters were packed under commercial conditions in glass jars with cocktail sauce and frozen. These samples were used by the NMFS marketing group in Gloucester to conduct market acceptance studies.

In the second test, commercially produced "steam and shake" oysters were frozen in cocktail sauce and in their own nectar in institutional sized packages. Laboratory taste tests indicated that these products were not significantly different in quality from either the laboratory prepared samples or the hand labor produced samples. So, it appears that frozen cooked oyster meats using the "steam and shake" method of removal represents a reasonable alternative to the oyster producer. The process can be automated or semiautomated, and the potential exists for using oysters which are not acceptable for hand shucking such as clusters or thin shelled oysters.

I specifically chose these areas to illustrate some technological advances which are currently being investigated and instituted by the shellfish industry. These types of technology represent a major opportunity for the industry to upgrade lower valued products and eliminate or reduce both raw material and automation restrictions. Although the processing concepts discussed are different, there is a central theme: increased efficiency; optimum utilization of raw material; and, most significantly, a change in direction away from the limited traditional product forms toward a broader product base with a much larger marketing potential. In short, a trend toward modern food science and technology.

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ASSESSMENT AND STATUS OF SEA SCALLOP *(PLACOPECTEN MAGELLANICUS)* POPULATIONS OFF THE NORTHEAST COAST OF THE UNITED STATES

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ABSTRACT

Landings of sea scallops (Placopecten magellanicus) *from the Northwest Atlantic reached record levels in 1977 when 24,000 metric tons of meats were harvested. The history of sea scallop landings, however, is one of large fluctuations. Catches have been affected by changes in population abundance, economic factors, and sociopolitical activities.*

The biology and fishery for sea scallops on Georges Bank and in the Middle Atlantic is reviewed. Trends in commercial landings for both the United States and Canada, the sole participants in the fishery, are described from 1887 to the present. Recent fishing patterns are related to resource evaluations derived from U.S.A. and Canadian research vessel sea scallop survey data.

An outstanding 1972 year-class resulted in significant increases in population biomass in the late 1970's in almost all areas on Georges Bank and in the Middle Atlantic, and has supported the recent intensive fishery. Recruitment has since been much poorer and with the exception of the Northern Edge and Peak region of Georges Bank, populations in most areas have substantially decreased.

Present management aspects are elucidated, both in regard to the resource, and the United States-Canada territorial boundary dispute. Future outlooks for the Georges Bank and Middle Atlantic populations are presented together with strategies which could contribute to increasing the long term potential yield of these resources.

INTRODUCTION

If we were asked to designate species names to calendar years as the Chinese do, in light of recent management events in particular U.S.A. east coast fisheries, we would classify 1977 as the year of the cod, 1978 as the year of the surf clam, and projecting ahead, 1979 as the year of the sea scallop. Clearly, events in the sea scallop fishery, which experienced the highest level of landings ever in 1977 (nearly 24,000 metric tons of meats, with U.S.A. landings about 11,000 tons — the highest in 15 years (Table 1)), have already received close scrutiny vis-a-vis the U.S.A. — Canadian ter-

TABLE 1. *United States and Canadian sea scallop landings (metric tons, meats) from the Northeast Coast of the United States (ICNAF Subarea 5 and Statistical Area 6), 1887-1977.*

Year	USA[1]	Year	USA	Canada[2]	Total
1887	112	1940	3,467		3,467
1888	91*	1941	144		144
1889	141	1942	3,258		3,258
1892	53	1943	2,508		2,508
1897	435	1944	2,209		2,209
1898	156	1945	2,590		2,590
*1899	24	1946	5,236		5,236
*1900	79	1947	6,647		6,647
1901	286	1948	7,546		7,546
1902	61	1949	8,299		8,299
*1903	62	1950	9,063		9,063
1904	216	1951	8,503	91	8,594
1905	200	1952	8,451	91	8,542
*1906	255	1953	10,713	136	10,849
*1907	236	1954	7,997	91	8,088
1908	834	1955	10,036	136	10,172
*1909	843	1956	9,102	317	9,419
*1910	919	1957	9,523	771	10,294
*1911	663	1958	8,608	1,470	10,078
*1912	842	1959	11,178	2,721	13,899
*1913	353	1960	12,065	3,390	15,455
*1914	386	1961	12,456	4,549	17,005
*1916	266	1962	11,174	5,694	16,868
1919	89	1963	9,044	5,877	14,921
1921	38	1964	7,721	5,901	13,622
1924	154	1965	9,104	7,027	16,131
1926	506	1966	7,237	7,641	14,878
1928	216	1967	4,646	5,007	9,653
1929	1,130	1968	5,474	5,227	10,701
1930	1,111	1969	3,362	4,304	7,666
1931	1,058	1970	2,613	4,082	6,695
1932	1,517	1971	2,593	3,894	6,487
1933	2,009	1972	2,654	4,162	6,816
1934	54	1973	2,401	4,208	6,609
1935	1,955	1974	2,721	6,115	8,836
1937	3,989	1975	4,422	7,387	11,809
1938	4,041	1976	8,712	9,745	18,457
1939	4,440	1977[3]	11,068	13,036	24,104

[1]USA landings from 1887-1960 taken from Lyles (1969); USA landings from 1961-1974 taken from Fishery Statistics of the United States, and from 1963-1976 taken from ICNAF Statistical Bulletins; 1977 landings were taken from ICNAF Sum. Doc. 78/VI/28 (Revised 15 June 1978). For 1964-1977, USA landings statistics were validated against New England Detailed Weighout Data, Northeast Fisheries Center.

[2]Canadian landings from 1951-1975 taken from ICNAF Statistical Bulletins and Hare (1977); 1977 landings were taken from ICNAF Sum. Doc. 78/VI/28 (Revised 15 June 1978).

[3]Provisional

*Maine landings only — from Baird (1956).

ritorial boundary dispute negotiations, and the stated intention of the newly established New England and Mid-Atlantic Regional Fishery Management Councils to implement a sea scallop management plan in early 1979.

In this paper we will briefly review several of the life history aspects of Northwest Atlantic sea scallop populations, and relate these data to historical trends in the fishery and to the current assessment of the status of the Georges Bank and Middle Atlantic scallop populations. We will also describe the present management regime and evaluate present and future population conditions based on the past dynamics of the resource and the concomitant fishery.

LIFE HISTORY ASPECTS

Sea scallops (*Placopecten magellanicus*) occur along the continental shelf of North America from the Strait of Belle Isle south to Cape Hatteras (Posgay, 1957). North of Cape Cod, scattered concentrations occur in shallow water often just below the low tide mark (Posgay, 1950; Dickie, 1953); further south aggregations are restricted to deeper, cooler offshore waters (Merrill, 1971). Sea scallops are intolerant of water temperatures above 20-22C (Posgay, 1953; Dickie, 1958), and hence the southern extremity of their range and their distribution in coastal estuaries are likely circumscribed by temperature (Dickie and Medcof, 1963; Merrill, 1971). Scallop beds sufficiently dense and extensive enough to support commercial fishing exist from Port au Port Bay, Newfoundland to the Virginia Capes (Posgay, 1957), generally at depths between 40 and 100 m (Merrill, 1962; Posgay, 1979). Although individualized movement of scallops within beds is common, tagging experiments (Baird, 1954, 1956; Dickie, 1953, 1955; Posgay, 1963) indicate an absence of directed population movements or seasonal migrations.

Spawning occurs in late summer or early fall, varying slightly between years and areas (Bourne, 1964). Spawning commences during July at the

southern extremity of the range (ie, North Carolina and Virginia) and proceeds northeastward as the year advances, ending in the northernmost regions by mid-October (MacKenzie et al., 1978). Sexes are separate, although occasionally hermaphrodites occur (Merrill and Burch, 1960; Naidu, 1970). Fertilization is external; individuals in the same general area may go from completely ripe to completely spent within a week (Posgay and Norman, 1958). The environmental stimuli triggering spawning are unknown, but may be associated with autumnal chilling precipitating thermal destratification and an increase in bottom temperature (Posgay, 1953), tidal cycles (Dickie, 1953), or temperature elevation and depression relative to thermal acclimation (Naidu, 1970).

Fertilized sea scallop eggs are buoyant, and undergo typical molluscan development as pelagic larvae (Merrill, 1961; Culliney, 1974). Duration of the planktonic phase in nature is unknown; laboratory culture experiments at 15 C indicated that spatfall is presumably related to prevailing surface current patterns during the pelagic period. Generalized sea surface circulation patterns (Figure 1) indicate a prevailing southwesterly flow from Georges Bank (Bumpus, 1973; Beardsley et al., 1976) suggesting that progeny of a given sea scallop aggregation are unlikely to settle out in the vicinity of the parental beds (Merrill, 1965; Posgay, 1979). Larvae spawned on Georges Bank, however, may frequently be retained there due to a semi-persistent gyre facilitating completion of metamorphosis in this region (Posgay, 1979). Sea scallop larvae have never been positively identified in plankton collections (Bourne, 1964) and thus it has not been feasible to trace their movements except from an inferential perspective.

Extensive concentrations of spatfall have yet to be located in natural environments. Small, juvenile scallops are rare in benthic samples although quantities of newly settled individuals have been found attached to navigation buoys (Merrill, 1961, 1965; Merrill and Posgay, 1967; Merrill and Edwards, 1976) and to bryozoan colonies (Baird, 1953). Recently, benthic sampling of selected areas on Georges Bank using a modified Smith-McIntyre grab resulted in the collection of 231 postlarval scallops, containing the smallest specimens (0.2 mm) ever obtained from the field (Larson and Lee, 1978). Normally, however, juvenile scallops are seldom taken in commercial or research gear. Submersible-vehicle and diver observations (Caddy, 1968; Edwards and Emery, 1968) reveal that these smaller individuals effectively avoid gear by swimming away from disturbance areas.

Sexual maturity may be attained as early as age 1, with the initial spawning occurring after deposition of the first growth ring (age 1½ or 2) (Naidu, 1970). Size at sexual maturity may vary from 23 to 75 mm (Naidu, 1970; Posgay, 1979) but fecundity

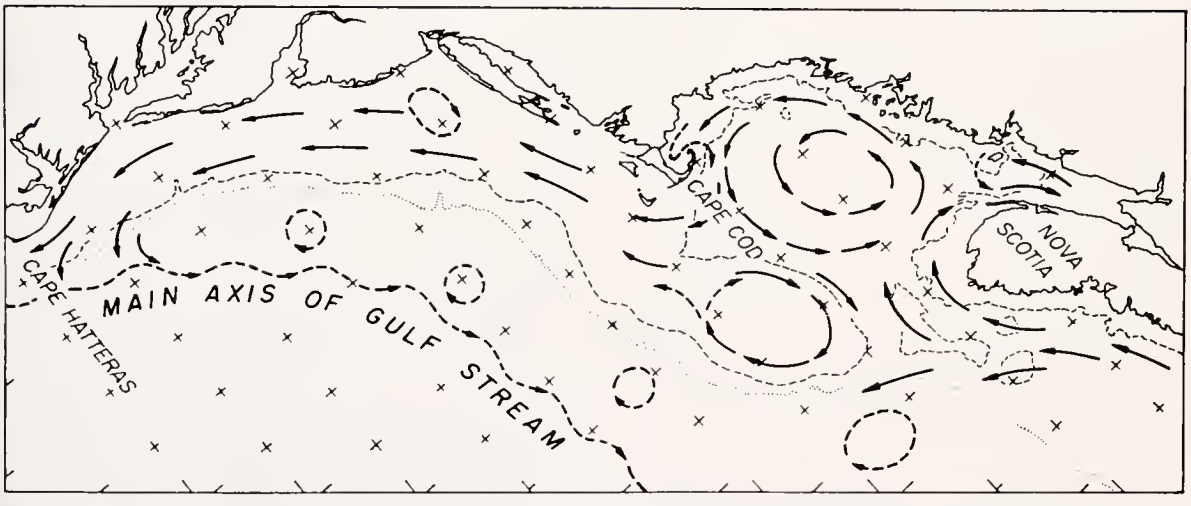

FIGURE 1. *Generalized pattern of sea surface current circulation, Nova Scotia to Cape Hatteras.*

of the younger age-groups contributes little to total egg production, By age 5 or 6, however, female scallops may each produce about 2 million eggs (Posgay, 1979).

Presently no biological evidence exists that implies stock differentiation within U.S.A. offshore sea scallop populations. Although minor growth rate differences exist between Georges Bank and Middle Atlantic populations, these appear to result from differing temperature regimes rather than genetic differences.

COMMERCIAL FISHERY

Sea scallops have been harvested off the coast of New England and the Canadian Maritime Provinces since colonial times (Bourne, 1964; Posgay, 1979). The U.S.A. commercial fishery originated in 1884 near Mt. Desert Island, Maine, when several nearshore, isolated beds were discovered (Smith, 1891; O'Brien, 1961); the first Canadia-sea scallop fishery developed in 1886 in Mahone Bay, Nova Scotia (Ganong, 1889).

U.S.A. sea scallop landings records exist from as far back as 1887 (Lyles, 1969; Table 1). The domestic fishery remained at a low level (< 1000 tons) until the early 1930's, when the extensive scallop beds on Georges Bank began to be more fully exploited (Doherty et al., 1964). By 1939 annual landings had reached 4,500 tons (Figure 2) due to the rapid development of the New Bedford scallop industry. Landings dropped sharply during World War II, but increased markedly afterward, reaching 9000 tons in 1950. During the next decade, U.S.A. landings remained fairly stable; between 1950 and 1958, domestic annual Georges Bank landings averaged about 7,465 tons while

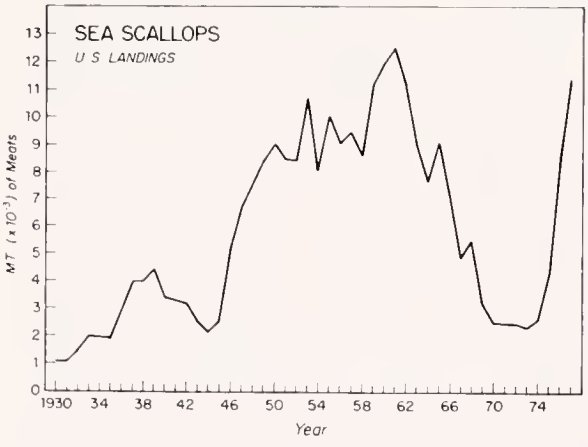

FIGURE 2. *Total reported United States sea scallop landings (metric tons, meats) from all Northwest Atlantic areas, 1930-1977.*

TABLE 2. *Historical trends in USA and Canadian sea scallop landings (metric tons, meats) from Georges Bank (ICNAF Div. 5z), 1944-1977*[1].

YEAR	USA	% of Total	Canada	% of Total	TOTAL
1944	1,814	100	—	0	1,814
1945	1,769	100	—	0	1,769
1946	4,036	100	—	0	4,036
1947	4,853	100	—	0	4,853
1948	4,580	100	—	0	4,580
1949	5,306	100	—	0	5,306
1950	5,442	100	—	0	5,442
1951	5,714	98	91	2	5,805
1952	5,488	98	91	2	5,579
1953	7,392	98	136	2	7,528
1954	7,029	99	91	1	7,120
1955	8,299	98	136	2	8,435
1956	7,937	96	317	4	8,254
1957	7,846	91	771	9	8,617
1958	6,531	85	1,470	15	8,001
1959	8,481	76	2,721	24	11,202
1960	9,932	75	3,390	25	13,322
1961	10,660	70	4,549	30	15,209
1962	9,690	63	5,694	37	15,384
1963	7,910	57	5,877	43	13,787
1964	6,296	52	5,901	48	12,197
1965	1,509	25	4,418	75	5,927
1966	892	16	4,861	84	5,753
1967	1,229	20	5,001	80	6,230
1968	1,049	18	4,805	82	5,854
1969	1,343	24	4,302	76	5,645
1970	1,421	26	4,082	74	5,503
1971	1,336	26	3,894	74	5,230
1972	823	17	4,146	83	4,969
1973	1,083	20	4,208	80	5,291
1974	930	13	6,115	87	7,045
1975	907	11	7,387	89	8,294
1976	1,770	15	9,726	85	11,496
1977	4,816	27	13,034	73	17,848

[1]SOURCE: 1944-1957, Caddy (1975); 1958-1976, ICNAF Statistical Bulletins; 1977, ICNAF Sum. Doc. 78/VI/28 (Revised 15 June 1978).

production from the Mid-Atlantic grounds averaged nearly 1,620 tons per annum (Lyles, 1969).

Beginning in the mid-1950's, the commercial fishery experienced major changes due to the development of the large-boat, offshore Canadian scallop fleet (Altobello et al., 1977). Canada entered the Georges Bank scallop fishery in 1951 but prior to 1956 Canadian offshore exploitation was sporadic (Doherty et al., 1963; Caddy and Lord, 1968). By 1957, however, Canadian landings comprised about 10 percent of the total Georges Bank sea scallop catch (Table 2; Figure 3). This year also marked the first occasion that offshore Canadian scallop landings significantly surpassed those from the traditional Canadian inshore Bay of Fundy and Gulf of St. Lawrence fisheries (Bourne, 1964).

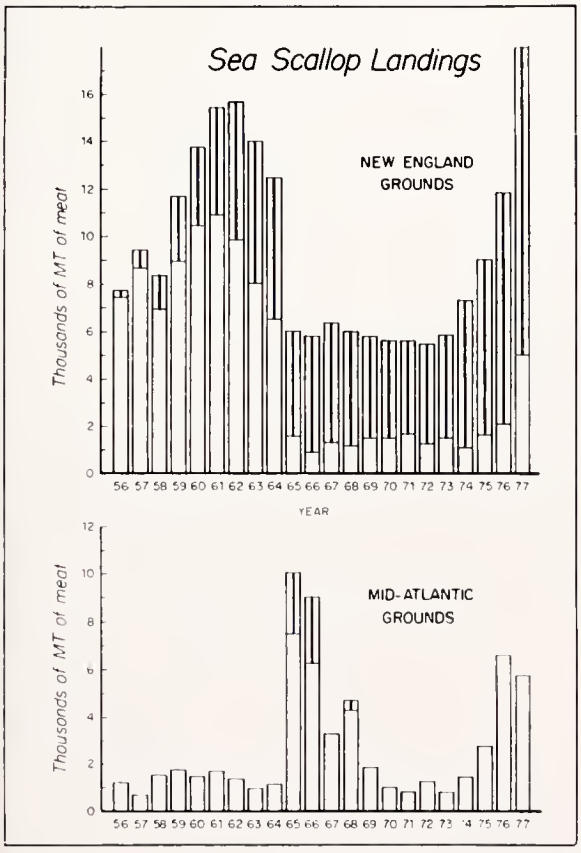

FIGURE 3. *Total reported United States and Canadian sea scallop landings (metric tons, meats) from Georges Bank and Mid-Atlantic fishing grounds, 1956-1977. The upper lined portions of the bars represent Canadian landings.*

In late 1959, an exceptionally abundant year-class (probably 1955) recruited to the Georges Bank fishery, and both U.S.A. and Canadian landings increased sharply (Table 2; Figure 3). In 1962, total landings reached 15,400 tons, nearly double that taken during 1958. Canadian participation in the fishery expanded greatly during this period; fleet size increased threefold and days fished incremented twofold between 1958-1962 (Bourne, 1964; Caddy and Lord, 1968). Resultingly, the percentage of the total Georges Bank catch harvested by Canada increased to 37 percent in 1962. By 1964, about half of the scallops taken from the Bank was by Canadian effort (Table 2).

In 1965, a highly successful year-class of scallops recruited to the Mid-Atlantic grounds (Posgay, 1968), resulting in a displacement of both U.S.A. and Canadian effort to the south. Ensuingly, total Mid-Atlantic landings rose to over 10,000 tons in 1965 (Figure 3); nearly a ninefold increase from 1964. U.S.A. Mid-Atlantic catches dropped slightly in 1966 (Table 3-Area 6) but increased Canadian landings from Virginia grounds resulted in a total catch of greater than 9,000 tons. In succeeding years, both U.S.A. and Canadian Mid-Atlantic harvests declined precipitously (Figure 3); by 1969, Canada had departed from the southern fishery and U.S.A. Mid-Atlantic production reverted to levels similar to those observed between 1956-1964.

The rapid development of the Mid-Atlantic fishery in 1965-66 impacted significantly on Georges Bank landings, particularly domestic catches. Between 1964 and 1967, the total Georges Bank scallop harvest declined from 12,200 to 6,200 tons (49% reduction-Table 2); U.S.A. landings from this fishery declined 80 percent while Canadian catches declined by only 15 percent. Accordingly, by 1965, 75 percent of the annual total Georges Bank scallop catch was taken by the Canadian fleet. Many of the U.S.A. (New Bedford) vessels, which fished almost exclusively on Georges Bank prior to entering the Mid-Atlantic fishery, never returned northward to any extent until 1977. Additionally, many domestic vessels left the fishery entirely, converting to groundfishing in response to rising fish prices. The New

TABLE 3. *USA sea scallop* (Placopecten magellanicus) *landings (metric tons, meat weight) from the Northwest Atlantic, 1961-1977, by ICNAF Statistical Area.*

Year	4	5Y	5Ze	5Zw	5Z	5NK	Total 5	6A	6B	6C	6NK	Total 6	Grand Total
1961		120			10,660		10,780					1,676	12,456
1962		103			9,690	3	9,796					1,378	11,174
1963	7	127			7,910		8,036					1,001[1]	9,044
1964	16	192	6,241	55	6,296		6,489					1,216[2]	7,721
1965		115	1,483	27	1,509		1,624					7,480[3]	9,104
1966		93	884	8	892		985					6,252	7,237
1967		80	1,221	8	1,229		1,309					3,337	4,646
1968		113	994	24	1,049		1,162	1,951	486		1,874	4,311	5,474
1969		123	1,325	19	1,343		1,466	553	307		1,045	1,896	3,362
1970		132	1,415	6	1,421		1,553	431	42		587	1,060	2,613
1971		362	1,329	7	1,336		1,698	274			621	895	2,593
1972		525	821	2	823		1,348	265	388	6	648	1,307	2,654
1973		460	1,080	3	1,083		1,544	143	95	11	609	857	2,401
1974		223	925	5	930		1,152	869	628	71		1,569	2,721
1975		746	857	50	907		1,653	1,641	899	228		2,769	4,422
1976		366	1,761	9	1,770		2,136	4,494	1,725	357		6,576	8,712
1977[4]		258	4,805	11	4,816	125	5,199	3,537	2,198	135		5,869	11,068

Sources:
1961-1974 Fishery Statistics of the United States.
1963-1976 ICNAF Statistical Bulletin.
1964-1977 Northeast Fisheries Center, New England Detailed Weightout Data, by Statistical Area

[1]973 from Fish. Stat. of U.S. (Mid-Atlantic and Chesapeake) + 28 from New England.
[2]1,079 from Fish. Stat. of U.S. (Mid-Atlantic and Chesapeake) + 137 from New England.
[3]3,509 from Fish. Stat. of U.S. (Mid-Atlantic and Chesapeake) + 3,971 from New England.
[4]Provisional (from ICNAF Sum. Doc. 78/IV/28, Revised 15 June 1978).

England sea scallop dredge fleet declined from 141 vessels in 1956 to 43 vessels in 1971 (U.S. Department of Commerce, 1973; Altobello et al., 1977).

During 1965-1973 on Georges Bank and 1969-1974 in the Mid-Atlantic, total commercial sea scallop landings stabilized at levels indicative of more normal annual recruitment patterns. Georges Bank catches averaged 5,600 tons annually (Table 2) while Mid-Atlantic catches averaged 1,300 tons per year (Table 3). Total landings from both fisheries, 1969-1974, amounted to only 7,200 per year — about the same annual production level recorded between 1946 and 1950, before Canadian entry into the offshore fishery (Lyles, 1969). Total U.S.A. sea scallop production in 1973 was 2,400 tons, the lowest in 29 years (Table 1).

Recruitment of the 1972 year-class was highly successful on both Georges Bank and in the Middle Atlantic (MacKenzie et al 1978). Total Georges Bank landings doubled between 1975 and 1977 (8,300 to 17,900 tons), as did Mid-Atlantic catches (2,800 to 5,900 tons). U.S.A. Georges Bank landings increased fivefold from about 900 tons in 1975 to 4,800 tons in 1977 (Table 3-Area 5Z), although the distribution of domestic landings from the major fishing grounds on the Bank remained similar to previous years (Table 4). The percentage of the total Georges Bank scallop harvest taken by the U.S.A. fishery, however, more than doubled in these years (11% in 1975 to 27% in 1977, Table 2).

Canadian Georges Bank landings rose from 7,400 tons in 1975 to 13,000 tons in 1977; the latter catch being an all-time peak for the Canadian offshore fishery (Table 1).

Total sea scallop landings in 1977, about 24,000

TABLE 4. *Geographical distribution of Georges Bank sea scallop landings for USA and Canada expressed as percentage of national yearly catch taken from the major fishing grounds, 1957-1977.*

Year	USA			Canada		
	South Channel	Southeast Part	Northern Edge and Peak	South Channel	Southeast Part	Northern Edge and Peak
1957	19	8	73	1	—	99
1958	19	7	74	—	—	100
1959	23	33	44	—	—	100
1960	18	45	37	—	—	100
1961	20	17	63	—	—	100
1962	18	19	63	—	—	100
1963	26	28	46	—	8	92
1964	41	31	28	—	2	98
1965	46	26	28	—	4	96
1966	81	3	16	—	—	100
1967	52	26	22	—	—	100
1968	70	14	16	—	—	100
1969	44	17	39	—	—	100
1970	76	11	13	1	—	99
1971	82	16	2	14	—	86
1972	76	8	16	10	—	90
1973	82	16	2	27	—	73
1974	85	13	2	9	5	86
1975	66	20	14	8	1	91
1976	89	8	3	8	—	92
1977	86	6	8	2	—	98

tons, were the highest on record. Total 1977 U.S.A. catches (11,100 tons) were the greatest in 15 years (Table 3; Figure 2), and provisional statistics for 1978 indicate that the current domestic harvest may be the highest ever, eclipsing the 1961 mark. Provisional Canadian landings during January-June 1978 approximated the 1977 landings, for the same period, implying that combined U.S.A.-Canadian sea scallop catches in 1978 may again exceed all previous annual levels..

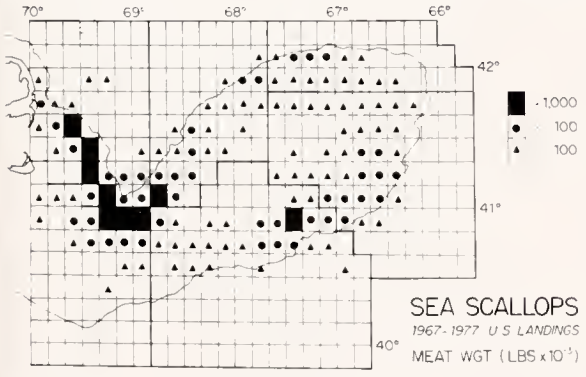

FIGURE 4. *Geographic distribution of United States sea scallop landings (thousands of pounds, meats) from Georges Bank, 1967-1977.*

Geographic distribution of U.S.A. sea scallop landings within subareas of Georges Bank and the Mid-Atlantic (Table 3; Figures 4 and 5) indicate that, in recent years, the South Channel area has been the major U.S.A. scalloping ground on Georges Bank, and that the New York Bight — Hudson Canyon region (Table 3-Area 6A) has produced most of the Mid-Atlantic catches. Prior to 1963, however, the Northern Edge and Peak region of Georges Bank accounted for the majority of both the U.S.A. Georges Bank production (Table 4) and total U.S.A. sea scallop catch. Canadian scallop exploitation on Georges Bank has always focused on the Northern Edge and Peak (Table 4). Historically (1944-1977), the Nor-

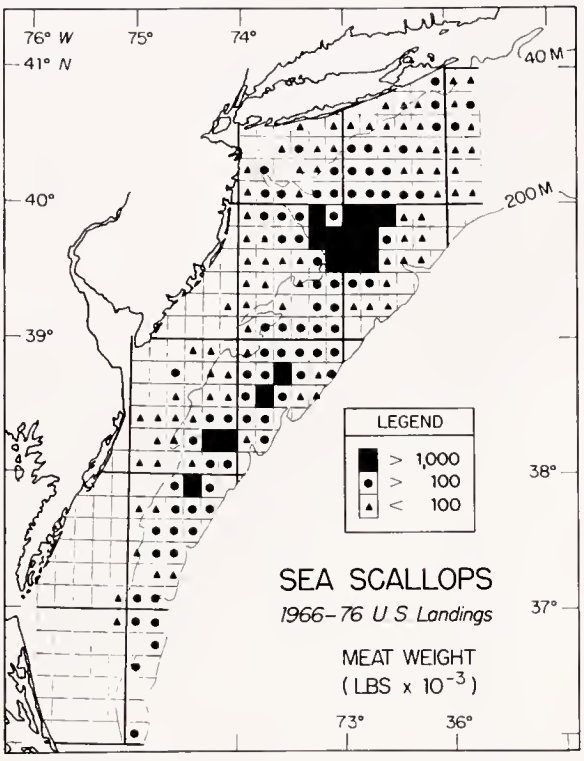

FIGURE 5. *Geographic distribution of United States sea scallop landings (thousands of pounds, meats) from the Mid-Atlantic, 1966-1976.*

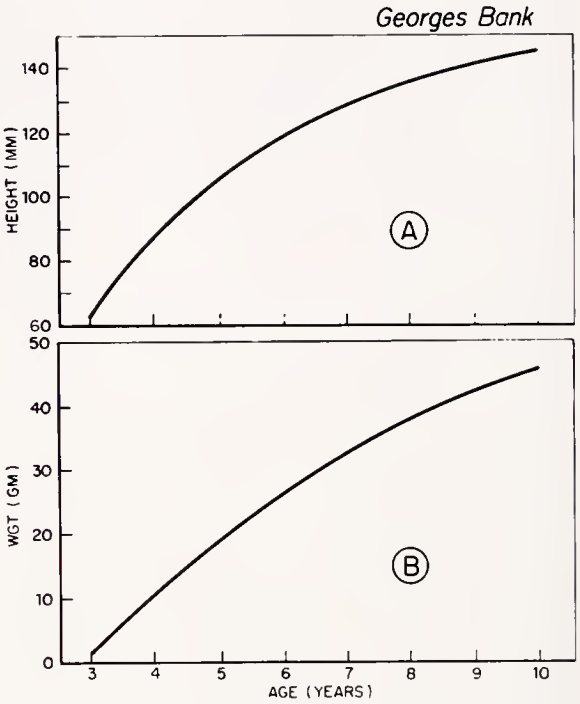

FIGURE 6. *Mean size, at age, for Georges Bank sea scallops. Shell height (mm) is presented in (A); meat weight (g) in (B).*

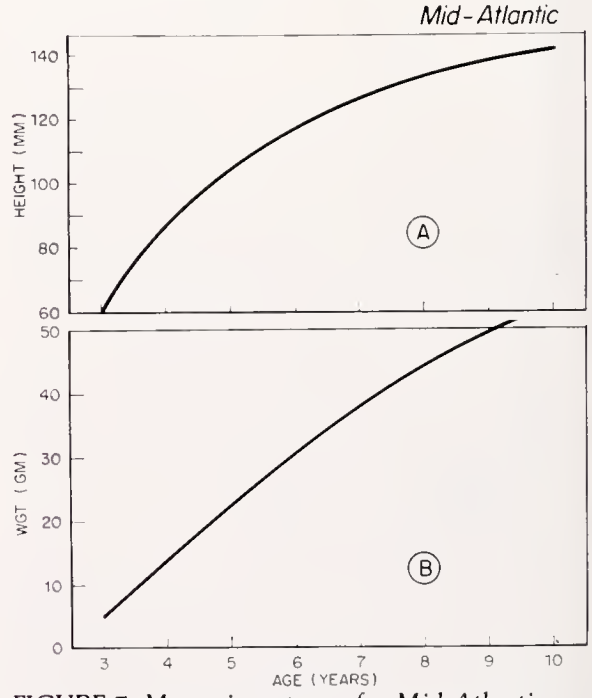

FIGURE 7. *Mean size, at age, for Mid-Atlantic sea scallops. Shell height (mm) is presented in (A); meat weight (g) in (B).*

thern Edge and Peak has produced greater than 69 percent of the total Georges Bank sea scallop catch.

GROWTH AND YIELD PER RECRUIT

Estimates of age and growth from shell samples and tagging experiments for both Georges Bank and Mid-Atlantic sea scallop populations (Posgay, 1953, 1963; Merrill and Posgay, 1964, 1967; Merrill et al., 1966) reveal that during the first several years of life, growth in both shell size and meat weight is rapid. Between ages 3 and 5, scallops commonly increase 50-80% in shell height and quadruple in meat weight (Figures 6 and 7), while about 10% die, per year, from natural causes (Merrill and Posgay, 1964). In this interval, the number of meats per pound is reduced from about 100 to 23 (Table 5). Between ages 8 and 9, annual growth falls to less than 10% per year, so that at age 8 (ca. 133 mm, 11 meats/lb) the increase in

TABLE 5. *Mean size (height and meat weight) at age for sea scallops* (Placopecten magellanicus) *from the Gulf of Maine, Georges Bank, and Mid-Atlantic populations. Number of meats per pound for all three areas is also presented.* *

	1	2	3	4	5	6	7	8	9	10	11	12
Gulf of Maine												
height (mm)[1]		26.90	56.05	79.42	98.18	113.23	125.30	134.99	142.76	149.00	154.00	158.02
meat weight (g)[2]		0.10	1.50	5.39	11.72	19.76	28.64	37.62	46.19	54.02	60.97	67.00
meat count/pound	4,536	302	84	39	23	16	12	10	8	7	7	
Georges Bank												
height (mm)[3]		25.63	61.95	87.87	106.37	119.57	128.99	135.71	140.51	143.93	146.37	148.12
meat weight (g)[4]		0.28	3.77	10.56	18.55	26.20	32.76	38.05	42.16	45.26	47.56	49.25
meat count/pound	1,620	120	43	24	17	14	12	11	10	10	9	
Mid-Atlantic												
height (mm)[5]		35.00	65.26	87.68	104.30	116.61	125.73	132.49	137.50	141.22	143.97	146.01
meat weight (g)[6]		0.77	5.11	12.54	21.27	29.86	37.56	44.05	49.32	53.48	56.72	59.19
meat count/pound	589	89	36	21	15	12	10	9	8	8	8	

[1]Derived from von Bertalanffy growth equation: $1_t = 174.32(1-e^{-.2202(t-1.2383)})$.
[2]Derived from age-weight relationship: $w_t = 96.006\,(1-e^{-.2202(t-1.2383)})^{3.664}$.
[3]Derived from von Bertalanffy growth equation: $1_t = 152.46\,(1-e^{-.3374(t-1.4544)})$.
[4]Derived from age-weight relationship: $w_t = 53.637(1-e^{-.3374(t-1.4544)})^{2.949}$.
[5]Derived from von Bertalanffy growth equation: $1_t = 151.84(1-e^{-.2297(t-1.1256)})$.
[6]Derived from age-weight relationship: $w_t = 66.691(1-e^{-.2297(t-1.1256)})^{3.0431}$.

*Sea scallops are spawned in the late summer-early autumn. An arbitrary birthdate of 1 October has been assigned to the date of spawning (Posgay and Norman, 1958), Hence, age in the above table refers to age as of 1 October.

TABLE 6. *Yield (grams, meat weight) per recruit for Georges Bank sea scallops as a function of instantaneous fishing mortality (F) and age at first capture (t_c). Natural mortality (M) = 0.1, and age at recruitment (t_r) = 2.0.*

Instantaneous rate of fishing mortality (F)	Age at first capture (t_c, years) and corresponding shell height (mm) and meat weight (g)																
	3.0 (62.0) (3.8)	3.5 (76.0) (6.9)	4.0 (87.9) (10.5)	4.5 (97.9) (14.5)	5.0 (106.4) (18.6)	5.5 (113.5) (22.5)	6.0 (119.6) (26.2)	6.5 (124.7) (29.6)	7.0 (129.0) (32.8)	7.5 (132.6) (35.6)	8.0 (135.7) (38.1)	8.5 (138.3) (40.2)	9.0 (140.5) (42.2)	9.5 (142.4) (43.8)	10.0 (143.9) (45.3)	10.5 (145.3) (46.5)	11.0 (146.4) (47.6)
0.1	13.6	14.0	14.2	14.4	14.3	14.2	13.9	13.6	13.2	12.7	12.2	11.6	11.1	10.5	9.9	9.4	8.8
0.2	15.7	16.8	17.6	18.2	18.5	18.6	18.6	18.4	18.0	17.6	17.0	16.4	15.8	15.1	14.5	13.8	13.1
0.3	15.3	16.8	18.1	19.1	19.8	20.2	20.3	20.3	20.1	19.7	19.2	18.7	18.0	17.4	16.7	16.0	15.2
0.4	14.4	16.3	17.9	19.2	20.1	20.7	21.1	21.2	21.0	20.7	20.3	19.8	19.2	18.6	17.9	17.2	16.5
0.5	13.4	15.5	17.4	18.9	20.1	20.9	21.4	21.6	21.6	21.3	21.0	20.5	19.9	19.3	18.6	17.9	17.2
0.6	12.5	14.9	16.9	18.6	20.0	20.9	21.5	21.8	21.9	21.7	21.4	20.9	20.4	19.8	19.1	18.4	17.7
0.7	11.7	14.2	16.5	18.3	19.8	20.9	21.6	21.9	22.1	21.9	21.7	21.2	20.7	20.1	19.5	18.8	18.0
0.8	11.1	13.7	16.1	18.0	19.6	20.8	21.6	22.0	22.2	22.1	21.9	21.4	20.9	20.4	19.7	19.0	18.3
0.9	10.5	13.2	15.7	17.8	19.4	20.7	21.5	22.0	22.3	22.2	22.0	21.6	21.1	20.5	19.9	19.2	18.5
1.0	10.0	12.8	15.3	17.5	19.3	20.6	21.5	22.1	22.3	22.3	22.1	21.8	21.3	20.7	20.1	19.4	18.7
1.1	9.6	12.4	15.0	17.3	19.1	20.5	21.5	22.1	22.3	22.4	22.2	21.9	21.4	20.8	20.2	19.5	18.8
1.2	9.2	12.1	14.8	17.1	19.0	20.4	21.4	22.0	22.4	22.4	22.3	21.9	21.5	20.9	20.3	19.6	18.9
1.3	8.9	11.8	14.5	16.9	18.8	20.3	21.4	22.0	22.4	22.5	22.3	22.0	21.6	21.0	20.4	19.7	19.0
1.4	8.6	11.6	14.3	16.7	18.7	20.2	21.3	22.0	22.4	22.5	22.4	22.1	21.6	21.1	20.5	19.8	19.1
1.5	8.3	11.3	14.1	16.6	18.6	20.1	21.3	22.0	22.4	22.5	22.4	22.1	21.7	21.1	20.5	19.9	19.1

TABLE 7. *Yield (grams, meat weight) per recruit for Mid-Atlantic sea scallops as a function of instantaneous fishing mortality (F) and age at first capture (t_c). Natural mortality (M) = 0.1, and age at recruitment (t_r) = 2.0.*

Instantaneous rate of fishing mortality (F)	Age at first capture (t_c, years) and corresponding shell height (mm) and meat weight (g)																
	3.0 (65.3) (5.1)	3.5 (77.3) (8.5)	4.0 (87.7) (12.5)	4.5 (96.6) (16.8)	5.0 (104.3) (21.3)	5.5 (110.9) (25.6)	6.0 (116.6) (29.9)	6.5 (121.5) (33.8)	7.0 (125.7) (37.6)	7.5 (129.4) (41.0)	8.0 (132.5) (44.0)	8.5 (135.2) (46.8)	9.0 (137.5) (49.3)	9.5 (139.5) (51.5)	10.0 (141.2) (53.5)	10.5 (142.7) (55.2)	11.0 (144.0) (56.7)
0.1	14.8	15.2	15.5	15.7	15.8	15.7	15.6	15.3	14.9	14.5	14.0	13.5	12.9	12.4	11.7	11.1	10.5
0.2	16.6	17.7	18.7	19.4	19.9	20.3	20.4	20.4	20.2	19.8	19.4	18.9	18.3	17.6	17.0	16.2	15.5
0.3	15.8	17.5	18.6	20.0	20.9	21.6	22.0	22.2	22.2	22.0	21.7	21.2	20.7	20.1	19.5	18.8	18.0
0.4	14.6	16.6	18.3	19.8	21.0	21.9	22.5	22.9	23.0	23.0	22.8	22.4	22.0	21.4	20.8	20.1	19.4
0.5	13.5	15.7	17.6	19.3	20.7	21.8	22.6	23.1	23.4	23.5	23.3	23.1	22.6	22.1	21.6	20.9	20.2
0.6	12.5	14.9	17.0	18.9	20.4	21.7	22.6	23.2	23.6	23.7	23.7	23.4	23.1	22.6	22.0	21.4	20.7
0.7	11.7	14.1	16.4	18.4	20.1	21.5	22.5	23.2	23.7	23.9	23.9	23.7	23.4	22.9	22.4	21.8	21.1
0.8	11.0	13.5	15.9	18.0	19.8	21.3	22.4	23.2	23.7	24.0	24.0	23.9	23.6	23.1	22.6	22.0	21.4
0.9	10.4	13.0	15.5	17.7	19.6	21.1	22.3	23.2	23.7	24.0	24.1	24.0	23.7	23.3	22.8	22.2	21.6
1.0	9.9	12.6	15.1	17.4	19.3	20.9	22.2	23.1	23.7	24.1	24.2	24.1	23.8	23.4	22.9	22.4	21.7
1.1	9.5	12.2	14.8	17.1	19.1	20.8	22.1	23.1	23.7	24.1	24.2	24.2	23.9	23.5	23.1	22.5	21.9
1.2	9.1	11.8	14.5	16.8	18.9	20.6	22.0	23.0	23.7	24.1	24.3	24.2	24.0	23.6	23.2	22.6	22.0
1.3	8.8	11.6	14.2	16.6	18.7	20.5	21.9	22.9	23.7	24.1	24.3	24.3	24.1	23.7	23.2	22.7	22.1
1.4	8.5	11.3	14.0	16.4	18.6	20.4	21.8	22.9	23.6	24.1	24.3	24.3	24.1	23.8	23.3	22.8	22.1
1.5	8.3	11.1	13.8	16.3	18.4	20.3	21.7	22.8	23.6	24.1	24.3	24.3	24.1	23.8	23.4	22.8	22.2

weight due to growth roughly balances the loss in weight due to natural mortality. Hence, if it were practical to wait until age 8 and then land all of these scallops, the greatest possible yield in weight for any given number of scallops recruiting into the fishery would be attained. This is analytically indicated in the yield per recruit calculations for the Georges Bank and Mid-Atlantic sea scallop populations (Table 6 and 7). Only slight gains, however, are achieved by delaying mean age of harvest beyond age 6. For both the Georges Bank and Mid-Atlantic populations, when size at first capture (age at first harvest) is held constant over a range of fishing mortality (Figures 8 and 9), two biological aspects become evident: (1) for most values of size at first capture, the highest yields occur at rather low fishing mortality values; and (2) for most values of fishing mortality, yield increases as size at first capture increases.

The current cull size in the U.S.A. scallop fishery is about 70-80 mm. For this size at first capture, maximum yield per recruit occurs at an instantaneous fishing mortality rate (F) of 0.2-0.3 (Tables 6 and 7). Hence, no gain in yield is realized by permitting F to exceed 0.3, and, in fact, potential yield actually decreases at higher fishing mortality rates.

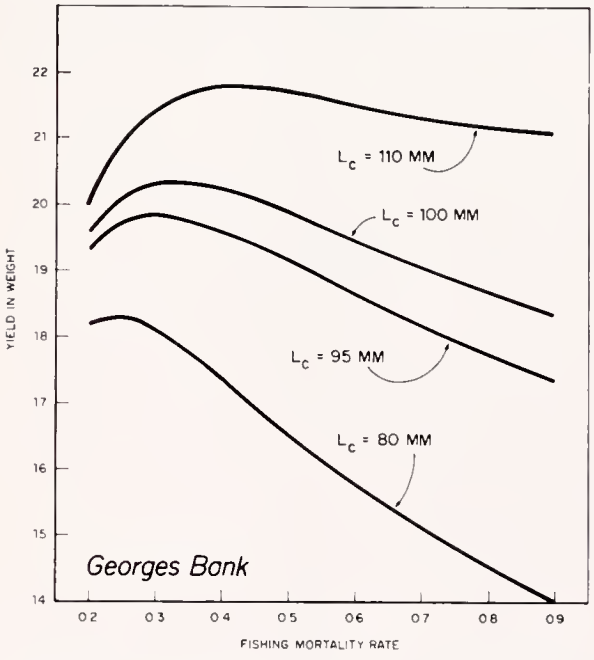

FIGURE 8. *Yield per recruit for Georges Bank sea scallops as a function of fishing mortality for various sizes (shell height) at first capture (L_c). Yield is expressed as grams per recruit.*

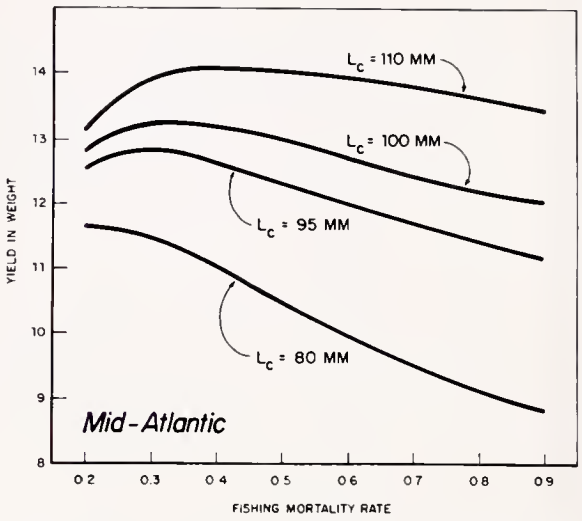

FIGURE 9. *Yield per recruit for Mid-Atlantic sea scallops as a function of fishing mortality for various sizes (shell height) at first capture (L_c). Yield is expressed as grams per recruit.*

STATUS OF THE STOCKS

Data on the condition of sea scallop populations in Northwest Atlantic offshore waters are available from both research vessel survey and commercial sources.

Sea scallop research vessel surveys have been conducted by the National Marine Fisheries Service in two series: an older survey series conducted between 1960 and 1968 in which collection of basic life history data was most often the major objective although relative abundance and catch composition was also assessed, and a newer series of surveys conducted in 1975, 1977, and 1978 to specifically evaluate, on both Georges Bank and in the Mid-Atlantic, relative abundance, population composition, and incoming recruiting year-class strength. Sea scallop research surveys were also performed in 1977 and 1978 by Canada, primarily in the Northern Edge and Peak region of Georges Bank. Dates, research vessels used, and the number of tows accomplished in both the older and newer research series (including the Canadian surveys) are presented in Tables 8 and 9.

TABLE 8. *NMFS sea scallop research vessel survey cruises on Georges Bank and in the Mid-Atlantic, 1960-1978.*

Date	Research Vessel	Cruise No.	Dredge Size	Ring Size	Tow Duration (min)	Georges Bank			Mid-Atlantic	No. of Tows
						South Channel	Southeast Part	Northeast Peak		
May 11-21, 1960	Delaware	60-7	10′[1]	3″	15				x	153[2]
May 23-29, 1960	Delaware	60-8	10′	2″	10	x	x	x		60
May 3-10, 1961	Delaware	61-7	10′	2″	10	x	x	x		184[3]
Sept. 22-31, 1961	Delaware	61-16	10′	2″	10	x	x	x		194
May 28-June 6, 1962	Delaware	62-6	10′	2″	10	x	x	x		184[4]
Sept. 11-20, 1962	Delaware	62-10	10′	2″	10			x		199[5]
May 13-17, 1963	Albatross	63-1	10′	2″	10	x	x			65
June 10-13, 1963	Albatross	63-3	10′	2″	10	x				96
Sept. 5-9, 1963	Albatross	63-6	10′	2″	10			x		26
May 13-22, 1964	Albatross	64-7	10′	2″	10		x	x		180
Sept. 7-15, 1964	Albatross	64-12	10′	2″	10	x	x			152[6]
May 3-13, 1965	Albatross	65-6	10′	2″	10		x	x		194[7]
Sept. 22-30, 1965	Albatross	65-13	10′	2″	10	x	x	x		167[8]
Aug. 11-23, 1966	Albatross	66-9	10′	2″	10		x	x		239[9]
Sept. 27-Oct. 16, 1966	Albatross	66-13	10′	2″	10				x	198
July 5-13, 1967	Albatross	67-12	10′	2″	10		x	x		210
Sept. 4-19, 1968	Albatross	68-14	10′	2″	10	x	x	x	x	322
Aug. 7-16, 1975	Albatross	75-8	10′	2″	15				x	100
Sept. 27-Oct. 3, 1975	Albatross	75-11	10′	2″	15	x	x	x		143
May 24-June 3, 1977	Albatross	77-03	10′	2″	15	x	x	x		144
Sept. 6-16, 1977	Albatross	77-08	10′	2″	15				x	189
Aug. 15-Sept. 1, 1978	Albatross	78-10	10′	2″	15	x	x		x	348

[1]A 30″ Digby dredge equipped with a ½ inch liner was also used
[2]Only 93 stations occupied
[3]Only 160 stations occupied
[4]Only 163 stations occupied
[5]Only 174 stations occupied
[6]Only 144 stations occupied
[7]Only 192 stations occupied
[8]Only 162 stations occupied
[9]Only 210 stations occupied

TABLE 9. *Sea scallop research vessel survey cruises on Georges Bank and in the Mid-Atlantic, 1975-1978.*

Date	Nation	Research Vessel	Number of Stations (Tows)					
			Georges Bank			Mid-Atlantic		
			South Channel	Southeast Part	Northern Edge and Peak	New York Bight	Delmarva	Virginia-North Carolina
8/7-8/16, 1975	USA	ALBATROSS IV	51	35	57			
9/27-10/3, 1975	USA	ALBATROSS IV				48	34	18
5/24-6/3, 1977	USA	ALBATROSS IV	40	27	77			
7/6-7/21, 1977	Canada	E.E. PRINCE	19	10	108			
9/6-9/16, 1977	USA	ALBATROSS IV				151	30	8
7/17-8/22, 1978	Canada	E.E. PRINCE	13	4	77			
8/15-9/1, 1978	USA	ALBATROSS IV	42	26	0	144	71	14

The recent U.S.A. surveys utilized a standard 10-foot (3.05 m) frame scallop dredge, equipped with a 2-inch (5.08 cm) ring bag, towed for 15 minutes at 3.5 knots. A stratified random sampling design was employed in both the 1977 and 1978 surveys; the 1975 survey used a transect design of stations. To compare the 1975 results with the later surveys, the 1975 station data were post-stratified before analysis into the sampling strata used in 1977 and 1978.

The 1977 and 1978 Canadian Georges Bank scallop surveys used a standard 8-foot (2.44 m) dredge, equipped with 3-inch (7.62 cm) diameter rings and a 1½-inch (3.81 cm) mesh nylon liner, towed for 0.5 nautical miles. Sampling stations were chosen on the basis of the amount of commercial effort expended in 10-minute statistical areas of latitude and longitude by both the Canadian and U.S.A. scallop fleets. Comparison of Canadian data with U.S.A. survey results was facilitated by post-stratification of the Canadian tow data, before analysis, into U.S.A. sampling strata. Canadian relative abundance indices (stratified mean number of scallops per tow) were further adjusted for the difference in tow distance between U.S.A. and Canadian standard tows. The mean distance towed per station in the 1977 and 1978 U.S.A. surveys was 0.88 and 0.89 nautical miles, respectively. Hence, the Canadian data were expanded by 1.76 (0.88/0.50) in 1977, and 1.78 (0.89/0.50) in 1978. The Canadian and U.S.A. relative abundance data were not standardized for size-selectivity differences between the sampling gears, although preliminary analysis of the 1977 results suggest that the Canadian lined-dredge was about twice as efficient in retaining pre-recruit scallops (< 70 mm shell height) as the U.S.A. dredge. Both dredges, however, appeared equally efficient in sampling scallops 70 mm and larger.

U.S.A. commercial information on quantity of scallop meats landed, fishing areas, and size composition of the catch was obtained from commercial landings statistics and NMFS dock-side commercial fisherman interviews. Comparable Canadian data were obtained from records supplied by Canadian sea scallop biologists. (R. Chandler and G. Jamieson, Env. Canada, St. Andrews N.B., personal communication, 1978).

Recent Catch Composition

U.S.A. commercial landings size-frequency data (shell height), from the South Channel region of Georges Bank and the New York Bight region in the Mid-Atlantic, 1975-1977, indicate the dependence of the domestic fleet during 1976 and 1977 on the 1972 year-class (Figures 10 and 11). Older age groups (larger sized scallops), well-represented in the 1975 landings and in earlier years, were of diminished importance in the 1976 and 1977 landings from both the northern and southern U.S.A. scallop fisheries.

Canadian commercial landings size-frequency data (shell height), 1975-1977, from the Northern Edge and Peak region of Georges Bank, derived from meat-weight port samples of the Canadian fleet (data provided by R. Chandler, Env. Can. Lab. St. Andrews N.B., personal communication, 1978), indicate a reliance on newly recruiting year-classes in the catch (Figure 12). The 1975 frequency-distribution clearly illustrates the importance of the 1972 year-class recruiting into the Canadian fishery, although older age groups were also represented. In 1976 and 1977, the 1972 year-class was also a major component of the landings, but the 1973 (and possibly 1974) year-classes appeared to be important as well.

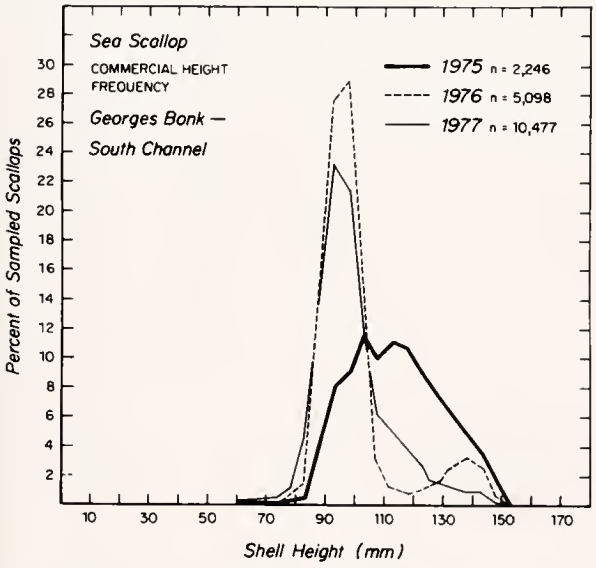

FIGURE 10. *United States commercial landings height-frequency distributions of sea scallops from the South Channel region of Georges Bank, 1975-1977.*

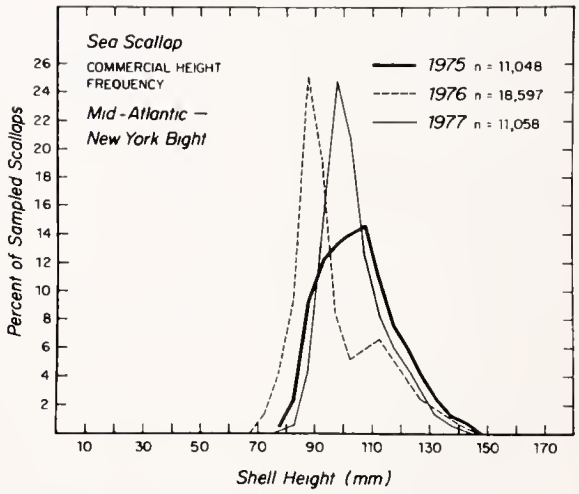

FIGURE 11. *United States commercial landings height-frequency distributions of sea scallops from the New York Bight region of the Mid- Atlantic, 1975-1977.*

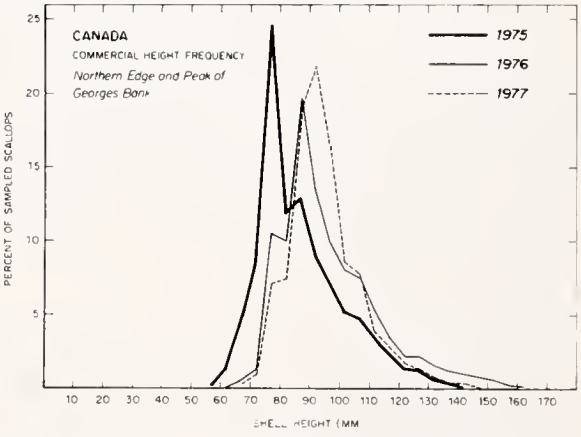

FIGURE 12. *Canadian commercial landings height-frequency distributions, derived from Canadian meat-weight distributions, from the Northern Edge and Peak region of Georges Bank, 1975-1977.*

Research Survey Size-Frequency Data

Size (shell height) frequencies from the 1975, 1977, and 1978 cruises on Georges Bank and in the Mid-Atlantic are summarized, by principal commercial fishery regions, in Figures 13 and 14. The 1975 results indicated that the 1972 year-class (40-60 mm shell height) was a very strong one in almost all major fishing areas on both Georges Bank and in the Mid-Atlantic. The 1977 and 1978

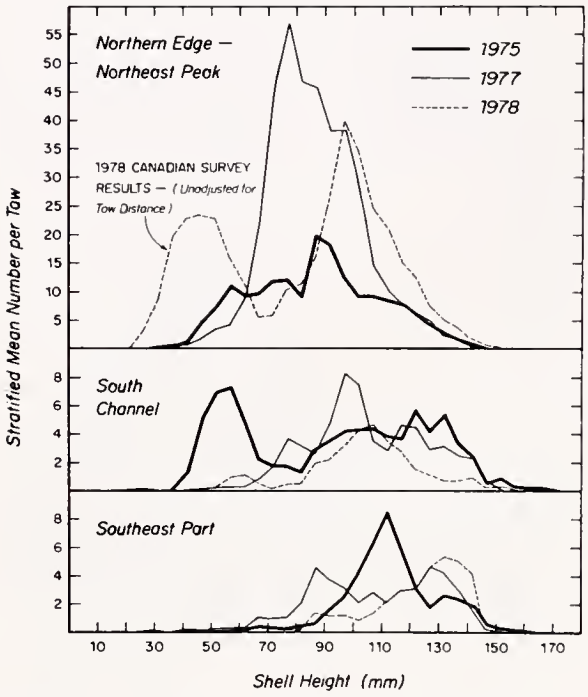

FIGURE 13. *United States research vessel survey height-frequency distributions of sea scallops from the three major fishing regions on Georges Bank (Northern Edge-Northeast Peak; South Channel; Southeast Part), 1975, 1977, and 1978. The 1978 Northern Edge-Northeast Peak data was derived from Canadian survey results.*

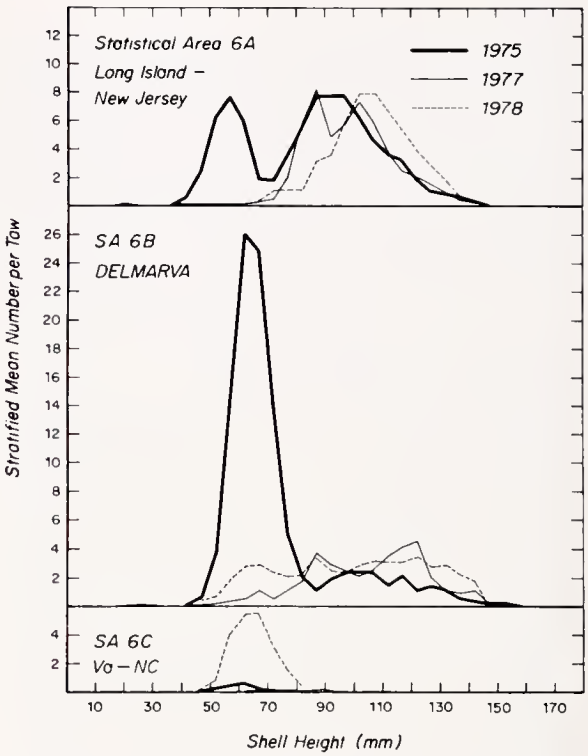

FIGURE 14. *United States research survey height-frequency distributions from the three major fishing regions in the Mid-Atlantic (Long Island-New Jersey; Delmarva; Virginia-North Carolina), 1975, 1977, and 1978.*

results further substantiated the relative strength of the 1972 year-class, but indicated also that apart from the Northern Edge and Peak region of Georges Bank, and the Virginia-North Carolina area in the Mid-Atlantic (1978 survey data), recruitment of the 1973, 1974, and 1975 year-classes was poor relative to the 1972 year-class. The virtual absence of these year-classes in the South Channel, Southeast Part, New York Bight, and Delmarva regions is striking.

The Northern Edge and Peak, which has consistently been the most productive area on Georges Bank (Bourne, 1964), has maintained high recruitment levels since 1972. The 1978 Canadian size-frequency survey data suggests that the 1975 year-class is much stronger than the 1974 year-class in this region (Figure 15) and apparently significantly exceeds that of the 1972 year-class (Figure 13).

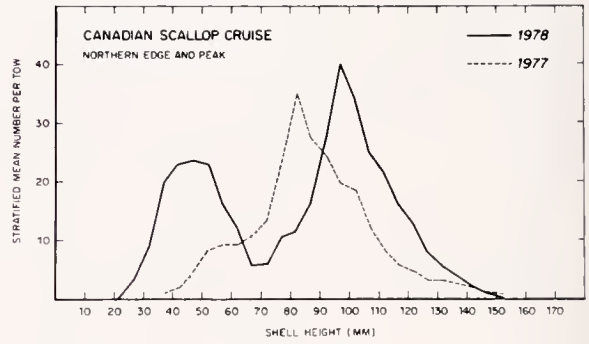

FIGURE 15. *Canadian research vessel survey height-frequency distributions from the Northern Edge and Peak region of Georges Bank, 1977 and 1978.*

A successful 1975 year-class is evident also in the Virginia-North Carolina region of the Mid-Atlantic (Figure 14). The 1972 year-class did not appear to be significant in this area in any of the

TABLE 10. *USA Sea scallop research survey abundance indices (stratified mean number per tow), 1975, 1977, and 1978, and total (USA and Canada) reported commercial landings (metric tons, meats and estimated number of scallops), and total commercial standardized effort (standard USA days fished), 1975-1978, from principal scallop grounds on Georges Bank (Subdiv, 5Ze). Survey indices are presented for pre-recruit (< 70 mm shell height), recruit (≥ 70 mm shell height), and total scallops per tow.*

		Stratified mean number per tow			Scallop landings (metric tons, meats)			Scallop landings (No. of scallops) $\times 10^{-3}$			Standard USA days fished		
		≥70 mm per tow	<70 mm per tow	Number per tow	USA	Canada	Total	USA	Canada	Total	USA	Canada	Total
Georges Bank													
South	1975	27.9	55.4	83.3	566	399	965	23,510	31,566[1]	55,076	735.1	438.7	1,173.8
Channel	1976	—	—	—	1,574	803	2,377	81,932	45,539	127,417	1,589.9	839.3	2,429.2
	1977	1.9	59.8	61.7	4,122	370	4,492	260,998	23,567[2]	284,565	3,888.7	336.8	4,225.5
	*1978	3.6	31.0	34.6	1,258	—	1,258	62,556	—	—	1,557.2	—	—
Southeast													
Part	1975	0.9	44.1	45.0	175	55	230	8,427	2,467[3]	10,894	227.3	57.0	284.3
	1976	—	—	—	141	17	158	8,064	717[4]	8,781	142.4	72.4	214.8
	1977	2.4	42.8	45.2	277	64	341	11,548	3,020	14,568	261.3	48.7	310.0
	*1978	1.5	36.3	37.8	50	—	50	2,486	—	—	55.2	—	—
Northern													
Edge and	1975	43.6	134.6	178.2	116	6,933	7,049	5,244	596,085	601,329	150.6	8,100.5	8,251.1
Peak	1976	—	—	—	45	8,906	8,951	2,854	570,534	573,388	45.5	9,334.8	9,380.3
	1977	42.7	349.4	392.1	407	12,600	13,007	18,156	871,972	890,128	384.0	11,585.3	11,969.3
	*1978	242.1	427.6	669.7[5]	729	5,710	6,439	30,695	—	—	572.2	—	—

*Landings and effort data for January-June only.
[1]Proration of landings done using mean weight of scallop derived from 1975 USA sea scallop research survey data from South Channel.
[2]Proration of landings done using Canadian mean weight of scallop derived from commercial weight-frequency distribution from South Channel for first six months of 1977.
[3]Proration of landings done using mean weight of scallop derived from 1975 USA sea scallop research survey data from Southeast Part.
[4]Proration of landings done using Canadian mean weight of scallop derived from commercial weight-frequency distribution from Southeast Part for first six months of 1976.
[5]1978 relative abundance indices on Northeast Edge and Peak derived from 1978 Canadian research survey data, adjusted for the distance differences between USA and Canadian standard tows (see text).

recent surveys (note the absence of larger-sized individuals in the 1977 and 1978 cruises), and hence the current 1975 year-class comprises the bulk of the population distribution.

Research Survey Relative Abundance Indices

Research survey relative abundance indices (numbers per tow) derived from the 1975, 1977, and 1978 Georges Bank and Mid-Atlantic cruises are presented in Tables 10 and 11, together with commercial landings, effort, and catch per effort data. Survey indices for all years have been tabulated for the pre-recruit (pre-commercial size: < 70 mm shell height) and recruited (commercially harvestable: ⩾ 70 mm shell height) components of the population, as well as for total numbers per tow.

On the Georges Bank grounds, the recent time series of survey abundance indices indicates that in the South Channel the relative abundance of the recruited segment of the population declined between 1975 and 1978. The recruited index drastically declined 48% from 59.8 in 1977 to 31.0 in 1978. Equally, the pre-recruit index dropped from 27.9 in 1975 to only 3.6 in 1978, reflecting the growth of the 1972 year-class into the exploitable sector of the population and the relative absence of subsequent recruitment. The fourfold increase in landings from the South Channel between 1975 and 1977 (965-4,492 tons), supported primarily by the 1972 year-class (Figure 10), has significantly decreased population size from the 1975 level.

Slight declines in both the total number per tow and the recruit number per tow transpired in the Southeast Part between 1975 and 1978 (16-18%

TABLE 11. *USA sea scallop research survey relative abundance indices (stratified mean number per tow), 1975, 1977 and 1978, and total reported commercial landings (metric tons, meats and estimated number of scallops) and total commercial standardized effort (standard USA days fished), 1975-1978, from principal scallop areas in the Mid-Atlantic. Survey indices are presented for pre-recruit (< 70 mm shell height), recruit (⩾70 mm shell height), and total scallops per tow.*

		Stratified Mean Number per tow			Scallop landings		
		Number < 70 mm per tow	Number ⩾ 70 mm per tow.	Total number per tow	Metric tons (meats)	Number of scallops ($x10^{-3}$)	Standard USA Days fished
Mid-Atlantic							
New York Bight	1975	25.0	57.2	82.2	1,641	105,288	1,908.1
	1976	—	—	—	4,494	345,484	4,048.6
	1977	0.7	52.3	53.0	3,537	230,971	2,899.2
	*1978	1.5	54.1	55.6	1,492	94,192	—
Delmarva							
	1975	70.2	39.3	109.5	899	61,134	1,045.3
	1976	—	—	—	1,725	136,724	1,554.1
	1977	2.4	34.4	36.8	2,198	115,747	1,801.6
	*1978	8.7	41.3	50.0	372	18,517	—
Virginia-No. Carolina							
	1975	1.7	0.1	1.8	228	13,897	276.7
	1976	—	—	—	357	27,496	321.6
	1977	0.1	0.1	0.2	135	8,256	110.7
	*1978	16.4	5.4	21.8	12	571	—

*Landings and effort data for January-June only from New England fishing vessels.

decrease). Recruitment, however, has remained relatively stable during the time period; the pre-recruit indices have ranged between 0.9 and 2.4. Landings doubled between 1976 and 1977, although the harvest of scallops from this area is minor compared to the landings from the South Channel and Northern Edge and Peak areas of the Bank.

Survey abundance indices from the Northern Edge and Peak, which were relatively high in 1975, substantially increased in the 1977 and 1978 surveys. Total numbers per tow almost quadrupled between 1975 and 1978; the pre-recruit and recruit indices similarly exhibited large increases between these years. The 1977 and 1978 pre-recruit indices suggest that recruitment of the 1974 and 1975 year-classes has been excellent. Total recruit abundance of scallops on the Northern Edge and Peak in 1978 was threefold greater than in 1975, despite a doubling of total landings during this period (Table 10).

The abundance indices of scallops on Georges Bank, using the older U.S.A. research survey time series with the 1975 and 1977 surveys added (Figure 16) indicate that abundance was high through 1962, dropped by over half during 1963-1965, and gradually declined until 1977, when it markedly increased due to the successfu-1972 year-class.

For the Mid-Atlantic scallop grounds, the survey indices exhibit almost comparable trends for the New York Bight and Delmarva regions (Table 11). Total numbers per tow, in both areas, substantially declined between 1975 and 1978 (-32% in the New York Bight -54% in Delmarva), while the relative abundance of the recruits remained stable. The pre-recruit indices, however, declined precipitously in each area, between 1975 and 1978 (25.0 to 1.5, New York Bight; 70.2 to 8.7, Delmarva). Commercial landings in 1976 and 1977 from both regions were 2-3 times higher than in 1975.

The 1978 relative abundance values for the Virginia-North Carolina area in the Mid-Atlantic were all (pre-recruit, recruit, and total numbers per tow) up significantly from preceding survey indices. Total relative abundance in 1978 was 12-fold higher than in 1975, due to a sharp increase in the number of pre-recruit scallops per tow (1.7 to

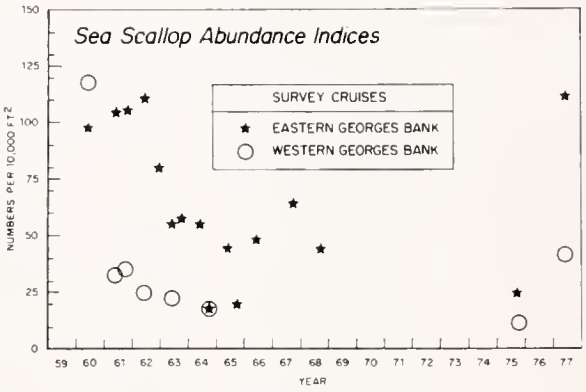

FIGURE 16. *Relative abundance indices of Georges Bank sea scallops derived from United States research vessel surveys, 1960-1977. Abundance is expressed as mean number of scallops larger than 70 mm (shell height) caught per 10,000 ft² dredged.*

16.4), indicative of a successful 1975 year-class of scallops in this area. While the 1978 total and recruit-indices are high compared to previous survey values observed in Virginia-North Carolina, they are generally low when compared with relative abundance levels, in any of the survey years, from other Mid-Atlantic areas.

Recent Commercial Effort (Days Fished)

Trends in commercial effort between 1975 and 1978 for each of the principal fishing grounds on both Georges Bank and in the Mid-Atlantic were analyzed to relate changes in survey values to effort variations. Data on U.S.A. effort was derived from port interview records comprising greater than 95% of the U.S.A. Georges Bank landings be een 1965-1977 (73% for 1975-78), and about 59% of the domestic Mid-Atlantic scallop catch (46% for 1975-78). These data represent U.S.A. vessels using scallop dredges and landing in New England ports (Tables 12, 13, and 14). Comparable Canadian Georges Bank data were obtained from J. F. Caddy (1975 and personal communication) and R. Chandler (personal communication).

Relative fishing power between the U.S.A. and Canadian fleet on Georges Bank was derived by a regression through the origin of the yearly mean catch per day values for the two fleets for the period 1965-1975 (Figure 17). The fishing power standardization coefficient was determined to be

TABLE 12. *USA sea scallop landings (metric tons, meats) from Georges Bank (Subdivision 5Ze), the Mid-Atlantic (Statistical Area 6), and Gulf of Maine (Division 5Y) fishing grounds, by vessel class tonnage category, 1965-1977. Data derived from vessels using scallop dredges and landing in New England ports.*

Area	Tonnage category	Year												
		1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Georges Bank (Subdivision 5Ze)	0-50	16.7	2.2	5.6	1.5	—	—	—	9.4	—	0.1	2.0	261.2	891.9
	51-150	1,275.5	733.7	921.4	819.3	917.2	993.1	766.1	467.3	678.1	557.4	491.4	931.4	2,545.3
	151-500	190.8	147.7	293.5	172.6	399.1	416.7	544.9	338.9	386.5	353.2	350.4	530.4	1,271.4
	Total	1,483.0	883.6	1,220.5	993.4	1,316.3	1,409.8	1,311.0	815.6	1,064.6	910.7	843.8	1,722.6	4,708.6
Mid-Atlantic (Area 6)	0-50	20.5	0.6	0.8	7.8	1.5	—	—	—	—	—	0.9	18.5	34.2
	51-150	3,608.1	3,530.3	1,547.5	1,601.3	481.7	189.9	72.1	289.2	42.5	397.1	659.7	1,042.4	929.7
	151-500	345.5	530.5	324.2	827.9	362.5	268.9	201.7	363.5	202.7	540.3	845.2	1,910.8	1,600.3
	Total	3,974.1	4,061.4	1,872.5	2,437.0	845.7	458.8	273.8	652.7	245.2	937.4	1,505.8	2,971.7	2,564.2
Gulf of Maine (Division 5Y)	0-50	99.5	92.6	77.5	108.5	107.8	114.6	222.8	487.0	393.8	210.6	734.1	349.0	252.1
	51-150	15.1	—	2.1	4.3	14.1	17.0	108.3	32.3	47.2	12.1	6.5	14.4	4.6
	151-500	—	—	—	—	—	—	26.6	4.9	18.6	—	—	—	—
	Total	114.6	92.6	79.6	112.8	121.9	131.6	357.7	524.2	459.6	222.7	740.5	363.4	256.7

TABLE 13. *USA sea scallop effort (days fished) on Georges Bank (Subdivision 5Ze), in the Mid-Atlantic (Statistical Area 6), and Gulf of Maine (Division 5Y) fishing grounds, by vessel class tonnage category, 1965-1977. Data derived from vessels using scallop dredges and landing in New England ports.*

Area	Tonnage category	Year												
		1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Georges Bank														
(Subdivision 5Ze)	0-50	11.1	11.4	17.3	3.5	—	—	—	20.4	—	0.2	10.5	308.1	1,028.4
	51-150	1,894.4	885.9	1,468.8	1,500.0	1,953.8	1,755.3	1,424.2	965.0	1,102.7	811.8	594.4	914.2	2,313.5
	151-500	213.4	167.4	400.3	304.2	759.5	822.9	988.7	805.9	739.6	576.3	494.9	516.8	1,120.7
	Total	2,118.9	1,064.7	1,886.4	1,809.7	2,713.3	2,578.2	2,412.9	1,791.3	1,842.3	1,388.3	1,099.8	1,739.1	4,462.6
Mid-Atlantic														
(Area 6)	0-50	48.1	3.0	5.0	38.9	3.5	—	—	—	—	—	3.3	59.8	70.7
	51-150	3,621.5	3,784.4	2,224.2	2,561.4	1,142.4	476.7	239.9	717.9	128.0	523.6	819.3	991.3	818.3
	151-500	312.8	524.7	452.0	1,196.2	700.4	516.0	479.5	688.5	428.0	700.9	923.8	1,625.9	1,216.1
	Total	3,982.4	4,312.1	2,681.2	3,796.5	1,846.3	992.7	719.4	1,406.4	556.0	1,224.5	1,746.4	2,677.0	2,105.1
Gulf of Maine														
(Division 5Y)	0-50	261.0	270.3	239.4	423.9	510.9	584.1	1,062.7	1,998.7	2,364.5	1,545.7	2,392.8	2,257.5	1,393.3
	51-150	20.4	—	2.7	12.8	53.7	49.7	116.1	90.5	128.8	33.9	14.0	32.0	4.1
	151-500	—	—	—	—	—	—	37.3	10.0	30.7	—	—	—	—
	Total	281.4	270.3	242.1	436.7	564.6	633.8	1,216.1	2,099.2	2,524.0	1,579.6	2,406.8	2,289.5	1,397.4

TABLE 14. *Observed USA sea scallop catch rates (metric tons of meats/day fished) from Georges Bank (Subdivision 5Ze), the Mid-Atlantic (Statistical Area 6), and Gulf of Maine (Division 5Y) fishing grounds, by vessel class tonnage category, 1965-1977. Data derived from vessels using scallop dredges and landing in New England ports.*

Area	Tonnage category	Year												
		1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Georges Bank (Subdivision 5Ze)	0-50	1.50	0.19	0.32	0.27	—	—	—	0.46	—	0.50	0.19	0.85	0.87
	51-150	0.67	0.83	0.63	0.55	0.47	0.57	0.54	0.48	0.61	0.69	0.83	1.02	1.10
	151-500	0.89	0.88	0.73	0.57	0.53	0.51	0.55	0.42	0.52	0.61	0.71	1.03	1.13
	Total	0.70	0.83	0.65	0.55	0.49	0.55	0.54	0.46	0.58	0.66	0.77	0.99	1.06
Mid-Atlantic (Area 6)	0-50	0.43	0.20	0.16	0.20	0.43	—	—	—	—	—	0.27	0.31	0.48
	51-150	1.00	0.93	0.70	0.63	0.42	0.40	0.30	0.40	0.33	0.76	0.81	1.05	1.14
	151-500	1.10	1.01	0.72	0.69	0.52	0.52	0.42	0.53	0.47	0.77	0.91	1.18	1.32
	Total	1.00	0.94	0.70	0.64	0.46	0.46	0.38	0.46	0.44	0.77	0.86	1.11	1.22
Gulf of Maine (Division 5Y)	0-50	0.38	0.34	0.32	0.26	0.21	0.20	0.21	0.24	0.17	0.14	0.31	0.15	0.18
	51-150	0.74	—	0.78	0.34	0.26	0.34	0.93	0.36	0.37	0.36	0.46	0.45	1.12
	151-500	—	—	—	—	—	—	0.71	0.49	0.61	—	—	—	—
	Total	0.41	0.34	0.33	0.26	0.22	0.21	0.29	0.25	0.18	0.14	0.31	0.16	0.18

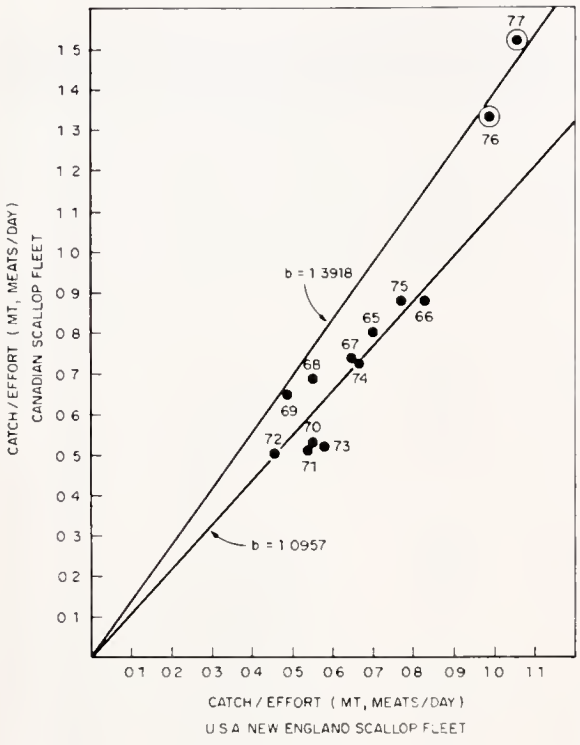

FIGURE 17. *Relative fishing power relationships between the United States and Canadian Georges Bank sea scallop fleets, 1965-1975, and 1976-1977.*

1.0957, a value almost identical to the 1.09 coefficient derived by Caddy (1975) for the years 1961-1971, and which he attributed to the ratio of the standard dredge widths between the two fleets.

The 1976 and 1977 Canadian-U.S.A. yearly catch/effort values, when plotted, were well above the 1965-1975 regression line (Figure 17). Regression of these two points through the origin results in a standardization coefficient of 1.3918, suggesting that the Canadian fleet has recently become 27% (1.3918/1.0957) more effective in capturing scallops relative to the U.S.A. Georges Bank fleet than previously. The cause for this apparent increase in relative efficiency is not known, although it may be due to procedural efficiency changes within the Canadian fleet precipitated by quota regulations imposed since 1976 by the Canadian government. Equally plausible is that the Canadian fleet may have fished on denser concentrations of scallops than U.S.A. vessels. The smaller size of acceptable scallops to the Canadian fishermen relative to the U.S.A. fleet may have been a causative factor as well.

U.S.A. effort on Georges Bank and in the Mid-Atlantic for 1975-1977 was expressed as standardized U.S.A. days fished by dividing total U.S.A. catches from each of the principal fishing grounds by the appropriate U.S.A. total yearly areal catch rate (Table 14). Canadian Georges Bank effort during 1975-1977 (provided by R. Chandler, personal communication) was adjusted to standardized U.S.A. days by multiplying the Canadian days fished by either 1.0957 (1975 value) or 1.3918 (1976 and 1977 values).

Standardized effort values for the three principal scallop grounds on Georges Bank, 1975-1978, are provided in Table 10. The South Channel and Northern Edge and Peak regions exhibited significant increases in total effort between 1975 and 1977; only minor increases in fishing effort were observed in the Southeast Part of the Bank during this period. Standard U.S.A. days fished by the U.S.A. fleet increased five-fold in the South Channel from 1975 to 1977 (735 to 3889), and 2.5 times on the Northern Edge and Peak (151-384). The absolute increase in U.S.A. effort on the Peak and Edge, however, is minor compared to recent Canadian effort in this region — Canada fished 8,100 standard days in 1975 and 11,585 standard days in 1978 (43% increase) on the Northern Edge and Peak.

Relative changes in total standardized effort, total landings, and survey abundance indices for the Georges Bank scalloping grounds, 1975-1978, are presented in Table 15. Between 1975 and 1977, total standardized effort (both U.S.A. and Canada) increased 260% in the South Channel, 9% in the Southeast Peak and 45% on the Northern Edge and Peak. The corresponding landings increases from each area were 365%, 48% and 85%, respectively. The effects of increased exploitation on the South Channel, coupled with a lack of substantive recruitment following the appearance of the 1972 year-class in 1975, were evidenced in the relative declines of the survey recruit (-44%) and pre-recruit (-87%) indices between 1975 and 1978. Relative changes in all effort, landings, and survey parameters in the Southeast Part during the last these years were small compared to either the Channel or Peak areas. This is not unexpected given the limited

TABLE 15. *Relative changes in total standardized effort (standard USA days fished), total landings (metric tons, and estimated numbers of scallops), and research survey relative abundance indices (total number per tow, recruit number per tow, and pre-recruit number per tow) from the principal scallop grounds on Georges Bank.*

	Time interval	Total standardized effort	Total landings (tons)	Total landings (number)	Total survey index	Survey recruit index	Survey pre-recruit index
Georges Bank							
South Channel							
	1975-1976	107%	146%	131%	—	—	—
	1976-1977	74%	89%	123%	—	—	—
	1975-1977	260%	365%	417%	-26%	8%	-93%
	1975-1978	—	—	—	-58%	-44%	-87%
Southeast Part							
	1975-1976	-24%	-31%	-19%	—	—	—
	1976-1977	45%	116%	66%	—	—	—
	1975-1977	9%	48%	34%	0%	-3%	167%[1]
	1975-1978	—	—	—	-16%	-18%	67%
Northern Edge							
and Peak	1975-1976	14%	27%	-5%	—	—	—
	1976-1977	28%	45%	55%	—	—	—
	1975-1977	45%	85%	48%	120%	160%	-2%
	1975-1978	—	—	—	276%	218%	455%

[1]Large percentage increase due to increase in numbers of pre-recruit scallops from 0.9 to 2.4 per tow, an overall generally low level.

fishing activity this region has been subject to in recent years.

The relative increases in effort and landings on the Northern Edge and Peak since 1975 have been much lower than the increases in any of the survey abundance indices. Between 1975 and 1977, total standardized effort increased by 45% and landings (tons) by 85%, while survey indices (total and recruit) increased by over 100%. The 1978 survey values show even more substantial percentage increases (1975-1978 comparisons) indicative of excellent recent recruitment.

Standardized effort values for the Mid-Atlantic scallop grounds, 1975-1978, and the relative changes in these values in relation to landings and survey indices are given in Tables 11 and 16, respectively. Effort increased in each of the three major grounds between 1975 and 1976; the most significant rise was observed in the New York Bight area (1,908 to 4,049 days, 112% increase). Annual U.S.A. effort on the New York Bight and Virginia-North Carolina grounds declined between 1976 and 1977, while effort in Delmarva increased slightly (1,554 to 1,802 days). In recent years, as previously, annual effort in the New York Bight area has exceeded the combined effort applied in the two more southerly Mid-Atlantic scallop areas.

Since 1975, each of the Mid-Atlantic areas has exhibited large relative changes in yearly effort and catch. Effort increased by greater than 50% between 1975 and 1977 in both the New York Bight and Delmarva regions. Concomitantly, landings from these grounds increased 116% and 144%, respectively. The 1976 and 1977 catches from each of these areas were the highest observed since 1968, when detailed records were first maintained on sub-areal landings within the Mid-Atlantic (Table 3). The relative increases in effort and catch in the New York Bight and Delmarva areas from 1975-1977 have been accompanied by only minor changes in the survey recruit indices. However, the pre-recruit indices declined by 94% in the Bight and by 88% in Delmarva between

TABLE 16. *Relative changes in total standardized effort (standard USA days fished), total landings (metric tons, and estimated numbers of scallops), and research survey relative abundance indices (total number per tow, recruit number per tow, and pre-recruit number per tow) from the principal scallop grounds in the Mid-Atlantic.*

	Time interval	Total standardized effort	Total landings (tons)	Total landings (numbers)	Total survey index	Survey recruit index	Survey pre-recruit index
Mid-Atlantic							
New York							
Bight	1975-1976	112%	174%	228%	—	—	—
	1976-1977	-28%	-21%	-33%	—	—	—
	1975-1977	52%	115%	119%	-36%	-9%	-97%
	1975-1978	—	—	—	-32%	-5%	-94%
Delmarva							
	1975-1976	49%	92%	124%	—	—	—
	1976-1977	16%	27%	-15%	—	—	—
	1975-1977	72%	144%	89%	-66%	-12%	-97%
	1975-1978	—	—	—	-54%	+5%	-88%
Virginia-North							
Carolina	1975-1976	16%	57%	98%	—	—	—
	1976-1977	-66%	62%	-70%	—	—	—
	1975-1977	-60%	-41%	-41%	-89%[1]	0%	-94%[1]
	1975-1978	—	—	—	1111%[2]	5300%[2]	865%[2]

[1]Large percentage decline due to decrease in small absolute numbers per tow (total index: 1.8-0.2; pre-recruit index: 1.7-0.1)
[2]Large percentage increases due to relatively modest increase in absolute number per tow (total index: 0.2-21.8; recruit index: 0.1-5.4; pre-recruit index: 0.1-16.4).

1975 and 1978. Clearly, the successful 1972 year-class has sustained the recent landings increases in these areas but subsequent good recruitment has not transpired.

The relatively high magnitude of recent changes in the Virginia-North Carolina effort, landings, and survey values belies the relative importance of this fishery *vis-a-vis* the two northerly Mid-Atlantic fisheries. Absolute annual effort and landings values in Virginia-North Carolina during 1975-1977 were an order of magnitude less than those of the other grounds. The substantial relative change between the 1977 and 1978 survey abundance indices, however, implies a significant population increase due to recent recruitment.

PRESENT MANAGEMENT REGIME

The present management regime on sea scallops differs between Canada and the U.S.A. The Canadians have implemented a series of regulations in an attempt to limit fishing effort and age at first capture (Table 17). The U.S.A. has no formal regulations, although union and industry practices are in place (New Bedford) that limit time at sea and crew size for individual vessels. For both nations (apart from the limited entry imposition on the Canadian fleet), management, formal or informal, is not really restrictive. The landings restrictions enacted by Canada are, in reality, quite liberal. Canadian regulations theoretically limit total annual catches to about 19,000 tons; only 13,000 tons were landed by Canadians in 1977. The 40 meat/lb count limitation enacted under Canadian regulations would not be restrictive on the U.S.A. fleet if it were imposed as the U.S.A. fleet lands larger scallops.

FUTURE OUTLOOK

Georges Bank Scallops

The scallop populations on Georges Bank have received increased fishing pressure during the last three years. Total landings increased two fold be-

TABLE 17. *Domestic Regulations On The Offshore Sea Scallop Fishery*

Canada

1. Vessel license to enter sea scallop fishery.
2. Limited Entry: 77 licensed vessels
   66 vessels fishing (8/77)
3. Vessel Trip Limits:
   a) 30,000 lbs. of meats/trip
   b) 180,000 lbs. of meats/4 month period
   c) 12 day maximum trip, dock to dock
4. Meat Size:
   a) Maximum of 40 meats/lb in landed catch
   b) 10% tolerance over the allowable count
   c) Meat count/trip — based on no less than 9 independent representative catch samples

USA

None

tween 1975 and 1978 as a result of recruitment of the highly successful 1972 year-class into the commercial fishery in the South Channel and Northern Edge and Peak, and substantial increases in fishing effort. Both the U.S.A. and Canadian scallop fleets have relied heavily on the strength of this year-class in their landings as indicated by commercial size-frequency distributions. Research survey relative abundance indices indicated in 1975 (and subsequently) that the 1972 year-class was very good; the recent yearly catches have corroborated this finding.

The 1978 Georges Bank survey abundance indices indicate that the current abundance of the commercially exploitable segment of the scallop population in the South Channel is less than in 1975, and in the Southeast Part is similar to that observed in 1975, and that the pre-recruit indices have either drastically declined (South Channel) or remained at a low level. These data imply that recent recruitment (after 1972 year-class) has been relatively poor in these regions, and that the present landings level (particularly for the South Channel) cannot be sustained without increasing fishing mortality.

A comparison of landings and effort between 1959-1964 (the previous period of exceptional recruitment and high landings on Georges Bank) and 1975-1977 (Table 18) suggests that by the end of 1978 approximately as much catch will have been removed from the South Channel and effort expended as occurred in the total six-year period from 1959-1964. The accumulated annual current effort may, in fact, have already exceeded former levels since present effort (both U.S.A. and Canada) may be more effective than in the early 1960's, resulting in an underestimate of current standard days fished compared to previous times. The intensive fishery prosecuted in the early period resulted in total Georges Bank landings declining by 50% between 1964 and 1965 (Table 2); total catches from the South Channel dropped 73% from 1964 to 1965 (Tables 3 and 4). Research vessel survey abundance indices (A. Posgay, unpub. data) correspondingly declined by greater than 50% (on both all of Georges Bank and in the South Channel) between 1964 and 1965. If the 1972 year-class is of the same magnitude as the one that supported the Georges Bank scallop fishery during the early 1960's, declines in landings and catch per effort, similar to those that occurred after 1964, are likely to occur in future years in the South Channel if current fishing patterns persist. Lack of recent successful recruitment in the Channel area implies that scallop abundance will decrease there in subsequent years. Even if the 1976 year-class proves to be strong (unlikely, given previous patterns of recruitment in which strong year-classes have appeared about once in a decade), this will not be significant in the South Channel landings until 1980, assuming present cull sizes.

The prospectus for the Southeast Part of Georges Bank, in the immediate future, is that this region should remain relatively stable if the current low levels of catch and effort are continued. Landings and effort were much higher in this area during 1959-1964 (Table 18) than at present. The relative absence of the 1972 year-class in the survey size-distributions during 1975-1978 (Figure 13) and continued low recruitment levels (Table 10) indicate that any intensified future exploitation will rapidly upset the current balance between low productivity and low annual sustained yields.

The Northern Edge and Peak yielded, during 1975-1978, approximately 55% of the total scallop harvest taken between 1959-1964, with about 59% of the previous total effort (Table 18). At current exploitation rates (1977), present annual ac-

TABLE 18. *Comparison of total sea scallop landings (metric tons, meats) and total commercial standardized effort (standard USA days fished) from the principal scallop grounds on Georges Bank (Subdiv. 5Ze), 1959-1964 and 1975-1977.*

Area	Statistic	Country	YEARS 1959	1960	1961	1962	1963	1964	Total	1975	1976	1977	Total
Georges Bank													
South Channel	Landings												
		USA	1,951	1,788	2,132	1,744	2,057	2,559	12,231	566	1,574	4,122	6,262
		Canada	—	—	—	—	—	—	—	399	803	370	1,572
		Total	1,951	1,788	2,132	1,744	2,057	2,559	12,231	965	2,377	4,492	7,834
	Effort												
		USA	1,968	1,447	1,734	1,613	2,007	2,732	11,501	735	1,590	3,889	6,214
		Canada	—	—	—	—	—	—	—	439	839	337	1,615
		Total	1,968	1,447	1,734	1,613	2,007	2,732	11,501	1,174	2,429	4,226	7,829
Southeast Part													
	Landings												
		USA	2,799	4,469	1,812	1,841	2,215	1,935	15,071	175	141	277	593
		Canada	—	—	—	—	470	118	588	55	17	64	136
		Total	2,799	4,469	1,812	1,841	2,685	2,053	15,659	230	158	341	729
	Effort												
		USA	2,823	3,618	1,474	1,702	2,161	2,065	13,843	227	142	261	630
		Canada	—	—	—	—	515	147	662	57	72	49	178
		Total	2,823	3,618	1,474	1,702	2,676	2,212	14,505	284	214	310	808
Northern Edge and Peak													
	Landings												
		USA	3,731	3,675	6,716	6,105	3,638	1,747	25,612	116	45	407	568
		Canada	2,721	3,390	4,549	5,694	5,407	5,783	27,544	6,933	8,906	12,600	28,439
		Total	6,452	7,065	11,265	11,799	9,045	7,530	53,156	7,049	8,951	13,007	29,007
	Effort												
		USA	3,765	2,974	5,463	5,644	3,550	1,865	23,261	151	45	384	580
		Canada	2,287	2,835	3,430	5,060	5,921	7,181	26,714	8,100	9,335	11,585	29,020
		Total	6,052	5,809	8,893	10,704	9,471	9,046	49,975	8,251	9,380	11,969	29,600

TABLE 18. *Continued*

Area	Statistic	Country	YEARS 1959	1960	1961	1962	1963	1964	Total	1975	1976	1977	Total
Total													
	Landings												
		USA	8,481	9,932	10,660	9,690	7,910	6,241	52,914	857	1,760	4,806	7,423
		Canada	2,721	3,390	4,549	5,694	5,877	5,901	28,132	7,387	9,726	13,034	30,147
		Total	11,202	13,322	15,209	15,384	13,787	12,142	81,046	8,244	11,486	17,840	37,570
	Effort												
		USA	8,556	8,039	8,671	8,959	7,718	6,662	48,605	1,113	1,777	4,534	7,424
		Canada	2,287	2,835	3,430	5,060	6,436	7,328	27,376	8,596	10,246	11,971	30,813
		Total	10,843	10,874	12,101	14,019	14,154	13,990	75,981	9,709	12,023	16,505	38,237

cumulated effort and catch will exceed the former total levels by the end of 1979. Recent successful recruitment, however, should maintain production at presently high levels for several years longer than this. If current fishing patterns change, as may be expected by shifts from the South Channel and the Mid-Atlantic regions to the Northern Edge and Peak, then the duration of high yield will be abbreviated accordingly. Since the Northern Edge and Peak, however, has exhibited more consistent annual recruitment than any other Northwest Atlantic sea scallop region, the biological risks associated with increased future exploitation appear relatively moderate.

In all regions on Georges Bank, scallops have been harvested, in recent years, at a size less than that producing maximum yield per recruit (about age 8, shell height 133 mm - Table 6). Since yield per recruit analyses (Figure 8) indicate that for most values of size or age at first capture, the highest yields occur at relatively low fishing mortality, *and* that at any level of fishing mortality, yield increases as size at capture increases, future decreases in fishing mortality and increases in cull size will increase yield per recruit.

Except for the Northern Edge, continuation of current levels of fishing effort may decrease scallop populations significantly below historical levels. While the lower range of formerly observed scallop stock sizes has not resulted in lowered recruitment, the general history of commercial fisheries indicates that careful observations are required as stock sizes decline to very low levels to evaluate threshold levels below which the probability of abundant recruitment becomes reduced.

Mid-Atlantic Scallops

Recent trends in landings and effort in the Mid-Atlantic scallop regions have generally paralleled those on Georges Bank; increases in catch and effort have resulted from recruitment of the 1972 year-class into the fishery. Research survey indices in the New York Bight and Delmarva areas indicated (in 1975 and afterward) an extremely high abundance of this year class (Table 11) and subsequent size-frequency distributions of commercial landings (Figure 11) and commercial annual catch/effort values (Table 14) have borne this out.

The 1978 Mid-Atlantic survey abundance in-

dices suggest that in the New York Bight and Delmarva regions the commercially exploitable segments of the population are as relatively abundant now as in 1975, but recruitment (pre-recruit indices) is substantially less. Hence, present landings and effort levels cannot be continued in the future without increasing fishing mortality. In the Virginia-North Carolina region, recent good recruitment will permit moderate increases in exploitation, in the next several years, without a significant reduction in abundance.

Comparison of landings and effort between 1965-1968 (the previous period of strong recruitment and intensive exploitation in the Mid- Atlantic) and 1975-1977 (Table 19) indicates that by the end of 1978 (given 1977 rate) about 77% of the catch and 62% of the effort that occurred from 1965-1968 will have been recorded. These data, by themselves, seem to suggest that the total Mid-Atlantic fishery could proceed for another year or two at current levels, assuming recruitment was equally strong in both time periods. However, much of the Canadian landings during 1965 and 1966 were taken from Virginia (Caddy and Lord, 1968), an area in which recruitment of the 1972 year-class was minor (Table 11, Figure 14). Equally, as in Georges Bank, current effort may be more effective than in the 1960's. The significant decrease in landings and effort between 1976 and 1977 suggests that commercial abundance levels may have already declined. This may be true, in spite of an apparent increase in commercial catch rate in 1977 (Table 14) since the fleet tends to concentrate on areas of high productivity, fish these down, and then move on to other high density areas. The implication here is that the number of highly productive areas has started to decline.

After 1968, total Mid-Atlantic landings declined 56% (1968-1969; 4,311 to 1,896 tons, Table 3). Given the poor recent recruitment pattern, noted in the historically important New York Bight and Delmarva regions, future declines in overall Mid-Atlantic scallop abundance are expected. Under current exploitation levels, this may first become widely apparent in 1979.

As in the Georges Bank scallop populations, Mid-Atlantic scallops have been taken before the size of maximum yield per recruit. Increasing age at the first capture and decreasing fishing mortality will be beneficial in increasing the total potential long-term yield from the resource.

Except for the Virginia-North Carolina area, current levels of fishing effort may reduce scallop populations significantly below those observed historically.

For all of the sea scallop populations off the northeast coast of the United States, given the data base currently available, the risks of the actual fishing mortality (F) being greater or less than desired are greater with catch limitations than with effort controls (days fished). Management strategies based on effort regulation are more robust than catch limits when the status of the resource is not precisely known and variations in production cannot be narrowly predicted.

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TABLE 19. *Comparison of total sea scallop landings (metric tons, meats) and total USA standardized effort (standard USA days fished) from all principal scallop grounds in the Mid-Atlantic (Statistical Area 6), 1965-1968, and 1975-1977.*

Statistic	Country	1965	1966	1967	1968	Total	1975	1976	1977	Total
Mid-Atlantic										
Landings	USA	7,480	6,252	3,337	4,311	21,380	2,768	6,576	5,870	15,214
	Canada	2,609	2,780	—	422	5,817	—	19	—	19
	Total	10,089	9,032	3,337	4,733	27,197	2,768	6,595	5,870	15,233
Effort										
	USA	7,480	6,651	4,767	6,736	25,634	3,230	5,924	4,812	13,967
	Canada	2,609	2,957	—	659	4,733	—	17	—	17
	Total	9,263	8,942	4,767	7,395	30,367	3,230	5,941	4,812	13,983

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LITERATURE CITED

Altobello, M.A., D.A. Storey, and J.M. Conrad. 1977. The Atlantic sea scallop fishery: A descriptive and econometric analysis. Mass. Agric. Expt. Sta., Res. Bull. 643: 80 p.

Baird, F.T. Jr. 1953. Observations on the early life history of the giant sea scallop *(Pecten magellanicus)*. Maine Dept. Sea Shore Fish., Res. Bull. 14: 2-7.

Baird, F.T. Jr. 1954. Migration of the deep sea scallop *(Pecten magellanicus)*. Maine Dept. Sea Shore Fish., Fish. Circ. 14: 8 p.

Baird, F.T. Jr. 1956. The sea scallop *(Pecten magellanicus)*. Maine Dept. Sea Shore Fish., Fish. Education Series, Unit No. 2: 11 p.

Beardsley, R.C., W. C. Boicourt, and D.V. Hansen. 1976. Physical oceanography of the New York Bight. Amer. Soc. Limnol. and Oceanogr. Spec. Symp. No. 2: 20-34.

Bourne, N. 1964. Scallops and the offshore fishery of the Maritimes. Fish. Res. Board Can. Bull. 145: 60 p.

Bumpus, D.F. 1973. A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6: 11-157.

Caddy, J.F. 1968. Underwater observations on scallop *(Placopecten magellanicus)* behavior and drag efficiency. J. Fish. Res. Board Can. 25: 2123-2141.

Caddy, J.F. 1975. Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. J. Fish. Res. Board Can. 32: 1305-1328.

Caddy, J.F., and E.I. Lord. 1968. Recent developments in the Georges Bank scallop fishery. Int. Comm. Northw. Atlant. Fish Redbook 1968 (III): 89-93.

Culliney, J.L. 1974. Larval development of the giant scallop, *Placopecten magellanicus* (Gmelin). Biol. Bull. 147: 321-332.

Dickie, L.M. 1953. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. Fish. Res. Board Can., MSS Rept. Biol. Sta. No. 526.

Dickie, L.M. 1955. Fluctuations in abundance of the giant scallop *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. 12: 797-857.

Dickie, L.M. 1958. Effects of high temperature on survival of the giant scallop. J. Fish. Res. Board Can. 15: 1189-1211.

Dickie, L.M., and J.C. Medcof. 1963. Causes of mass mortalities of scallops *(Placopecten magellanicus)* in the southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. 20: 451-482.

Doherty, R.M., G.P. Draheim, D.J. White, and C.L. Vaughn. 1963. Sea scallop industry of Canada. Comm. Fish. Rev. 25(7): 11-16.

Doherty, R.M., G.P. Draheim, D.J. White, and C.L. Vaughn. 1964. Economic study of sea scallop production in the United States and Canada. Fish. Ind. Res. 2(3): 57-79.

Edwards, R.L., and K.O. Emery. 1968. The view from a storied sub. The 'Alvin' off Norfolk, Va. Comm. Fish. Rev. 8-9: 48-55.

Ganong, W.F. 1889. The economic mollusca of Acadia. Bull. Nat. Soc. New Brunswick No. 8: 116 p.

Hare, G.M. 1977. Atlas of the major Atlantic coast fish and invertebrate resources adjacent to the Canada-United States boundary areas. Fish. and Mar. Serv. Can., Tech. Rept. 681: 97 p.

International Commission for the Northwest Atlantic Fisheries (ICNAF). 1978. Provisional nominal catches in the Northwest Atlantic, 1977. ICNAF Summ. Doc. 78/VI/28 (Revised 15 June 1978), Serial No. 5268: 51 p.

Larsen, P.F., and R.M. Lee. 1978. Observations on the abundance, distribution and growth of postlarval sea scallops, *Placopecten magellanicus*, on Georges Bank. The Nautilus 92: 112-116.

Lyles, C.H. 1969. Historical catch statistics (shellfish). U.S. Fish. Wildl. Serv., Comm. Fish. Statistics No. 5007: 116 p.

MacKenzie, C.L., A.S. Merrill, and F.M. Serchuk. 1978. Sea scallop resources off the Northeastern U. S. Coast. Marine Fish. Rev. **40**: 19-23.

Merrill, A.S. 1961. The sea scallop fishery. Bull. Amer. Malacol. Union **28**: 14.

Merrill, A.S. 1962. Abundance and distribution of sea scallops off the Middle Atlantic coast. Proc. Nat. Shellf. Assoc. **51**: 74-80.

Merrill, A.S. 1965. The benefits of systematic biological collecting from navigation buoys. ASB Bull. **12**: 3-8.

Merrill, A.S. 1971. The sea scallop. Ann. Rept. (1970) Amer. Malacol. Union: 24-27.

Merrill, A.S., and J.B. Burch. 1960. Hermaphroditism in the sea scallop, *Placopecten magellanicus* (Gmelin). Biol. Bull. **119**: 197-201.

Merrill, A.S., and R.L. Edwards. 1976. Observations on mollusks from a navigation buoy with special emphasis on the sea scallop, *Placopecten magellanicus*. The Nautilus **90**: 54-61.

Merrill, A.S. and J.A. Posgay. 1964. Estimating the natural mortality rate of the sea scallop *(Placopecten magellanicus)*. Int. Comm. Northwest Atl. Fish. Res. Bull. **1**: 88-106.

Merrill, A.S., and J.A. Posgay. 1967. Juvenile growth of the sea scallop, *Placopecten magellanicus*. Ann. Rept. (1967) Amer. Malacol. Union: 51-52.

Merrill, A.S., J.A. Posgay, and F.E. Nichy. 1966. Annual marks on shell and ligament of sea scallop *(Placopecten magellanicus)*. U.S. Fish. Wildl. Serv., Fish. Bull. **65**: 299-311.

Naidu, K.S. 1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. Can. J. Zool. **48**: 1003-1012.

O'Brien, J.J. 1961. New England sea scallop fishery and marketing of sea scallop meats, 1939-1960. U.S. Dept. Interior, Bur. Comm. Fish., Market News Service: 48 p.

Posgay, J.A. 1950. Investigations of the sea scallop, *Pecten grandis*, p. 24-30. *IN* Third Report on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth of Massachusetts, Dept. Nat. Res., Div. Mar. Fish.

Posgay, J.A. 1953. The sea scallop fishery, p. 9-24. *IN* Sixth Report on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth of Massachusetts, Dept. Nat. Res., Div. Mar. Fish.

Posgay, J.A. 1957. The range of the sea scallop. The Nautilus **71**: 55-57.

Posgay, J.A. 1963. Tagging as a technique in population studies of the sea scallop. Int. Comm. Northwest Atl. Fish., Spec. Publ. **4**: 268-271.

Posgay, J.A. 1968. Trends in the Atlantic sea scallop fishery. Comm. Fish. Rev. 30: 24-26.

Posgay, J.A. 1979. Sea Scallop *Placopecten magellanicus* (Gmelin). *IN* Grosslein, M.D., and T. Azarovitz (eds), Fish Distribution. MESA New York Bight Monograph No. 15, New York Sea Grant Institute, New York.

Posgay, J.A., and K.D. Norman. 1958. An observation on the spawning of the sea scallop, *Placopecten magellanicus* (Gmelin), on Georges Bank. Limnol. Oceanogr. **3**: 142.

Smith, H.M. 1891. The giant scallop fishery of Maine. Bull. U.S. Fish. Comm. **4**: 313-335.

U.S. Department of Commerce. 1973. Scallops, 1930-1972. Current Fish. Statistics No. 6127: 35 p.

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ABSTRACTS OF TECHNICAL PAPERS PRESENTED AT THE 1978 ANNUAL MEETING

A THREE MONTH GROWTH AND MORTALITY STUDY OF NORMAL AND NEOPLASTIC *MYA ARENARIA* CROSS-TRANSPLANTED BETWEEN CLEAN AND OIL-IMPACTED AREAS

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Six hundred and eighty soft-shell clams from 4 different populations were cross-transplanted between a clean site (Winnapaug Pond, RI) and an oil-impacted former Navy dumpsite (Allen Harbor, RI) in a three month study to determine the effects of environment and neoplasia on growth and mortality. Clams were weighed and measured to analyze growth, diagnosed for neoplasia and analyzed for hydrocarbon content before and after transplantation. The incidence of neoplasia at the clean and oil-impacted sites were approximately equal. Differences in growth were significant ($P<0.05$) between sites, between populations, and between neoplastic and normal individuals. Significant differences in mortality were found between sites and between populations. Mortality was greater in neoplastic clams than in normal clams, but the difference was not significant, possibly due to the small sample size or the chronic nature of the disease. Growth was reduced and mortality was greater at Allen Harbor, probably due to a combination of 1) stress of transplanting, 2) less favorable sediment type characteristics, and 3) the effect of pollutants. Neoplasia reduced individual growth by an average of 20% at Winnapaug Pond and by 50% at Allen Harbor. Assuming no mortality, it was calculated that soft-shell clam production at Allen Harbor was reduced by as much as 1/5 due to the effects of neoplasia.

COMPARISON OF THE GROWTH AND SURVIVAL OF RED SWAMP CRAWFISH (*PROCAMBARUS CLARKII* (GIRARD)) AND WHITE RIVER CRAWFISH (*PROCAMBARUS ACUTUS ACUTUS* (GIRARD))*

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Red swamp crawfish (*Procambarus clarkii* (Girard)) and white river crawfish (*Procambarus acutus acutus* (Girard)) were stocked in modified 55-gallon containers with constant water flow at the following ratios (total 12 crawfish per container): 100%: 0% (*P. clarkii*:*P. a. acutus*) 67%:33%; 50%:50%: 33%:67%; and 0%:100%. Initial size was approximately 2.5 cm for both species. The experiment began on 8 January 77 and ended on 29 April 77. Comparison of growth revealed that *P. a. acutus* grew slightly larger than *P. clarkii* (6.2 cm versus 6.0 cm after 9 weeks; 9.1 cm versus 8.7 cm after 15 weeks). Survival of each species was similar (no significant differences—$P<0.5$) regardless of the original ratios at the beginning of the experiment. These values were: 9 weeks, *P. clarkii*—66% and *P. a. acutus*—55%; 15 weeks, *P. clarkii*—24% and *P.*

a. acutus—13%. Mean densities through time were: start—54/sq. meter; 9 weeks—33/sq. meter; and 15 weeks (end)—10/sq. meter.

*This research was partially supported by the La. Ag. Expt. Sta.

AN APPROACH TO THE MANAGEMENT OF A HARD CLAM RESOURCE

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Increased fishing pressure and the closure of areas to the harvesting of shellfish have posed a threat to the continued existence of the hard clam fishery in Great South Bay, New York. In an attempt to maintain the productivity of this resource, a comprehensive shellfish management program has been established at the local governmental level which applies basic fisheries research data to practical management problems. This paper discusses the methods by which information generated from various research projects is used to plan stocking programs and alternative management strategies. Specific research projects discussed include a yearly analysis of harvest and catch per unit effort, and a hard clam population survey. As a result of these, a number of stocking programs, including a hard clam transplant, spawner transplant and a mariculture project are planned and carried out on an annual basis. The data base developed thus far is presented, as well as recommendations for additional research that will be required for improved management of the resource.

INFECTIONS OF *TYLOCEPHALUM* IN COMMERCIAL OYSTERS AND THREE PREDACEOUS GASTROPODS OF THE EASTERN GULF OF MEXICO

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Uniacetabulo-plerocercoids of *Tylocephalum* sp.*sensu* Burton (1963) (Cestoda; Cephalobothriidae) are reported from the American oyster, *Crassostrea virginica* (Gmelin) (Bivalvia; Ostriedae), and three of its gastropod predators in the eastern Gulf of Mexico: the lightning whelk, *Busycon contrarium* (Conrad) (Gastropoda; Melongenidae), the apple murex, *Murex pomum* Gmelin (Muricidae), and the southern oyster drill, *Thais haemastoma canaliculata* (Gray) (Muricidae). Sixty of 138 oysters (43%) from 12 of 17 localities, 79 of 90 whelks (88%) from 14 of 15 localities, 32 of 33 murexes (97%) from 6 of 6 localities and 23 of 53 drills (43%) from 5 of 8 localities harbored encysted *Tylocephalum* plerocercoids. Those predaceous gastropods probably acquire plerocercoids from infected oysters. No pathological conditions were observed in oysters or their predators.

CHRONIC INFECTIONS OF *MINCHINIA NELSONI* (MSX) IN DELAWARE BAY OYSTERS

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Infection periods for the oyster parasite, *Minchinia nelsoni* (MSX) occur regularly each summer in enzootic areas. Oysters inhabiting these waters are therefore exposed to infective particles every year and exhibit a distinct annual infection cycle which is dictated by the timing and intensity of the infective period, the oysters' resistance to the disease, and various ambient influences including salinity and temperature.

Many infections gained at the start of one infection cycle appear to be lost at the end of that cycle, approximately one year later. Some are retained into the new cycle. At the same time, new infections, from a second cycle, are being acquired. In lower Delaware Bay where oysters are subjected to annual reinfection by MSX, it has frequently been impossible to distinguish recent infections from those held over from previous years. In order to separate the two, heavily infected oysters from Delaware Bay were taken to an MSX-free

area of the New Jersey coast. Since infections subsequently seen in these oysters could have been acquired only in Delaware Bay during a particular infective period, it was possible to accurately gauge the percentage of infections held over from year to year as well as the age of the infection and thus, the duration of the host-parasite relationship.

Oysters moved to the MSX-free area at the end of the infection cyle exhibited a pronounced infection dropout, but this proved to be only temporary, for some infections reappeared later in the year. In fact, chronic infections exhibited an annual prevalence and intensity pattern which was very similar to that found in oysters undergoing annual reinfection in Delaware Bay. Localized epithelial lesions predominated in early spring and mid-summer, while general infections were found most often in early winter and late spring. Chronic infections became localized (or sub-patent), relapsed into general infections, then became localized or sub-patent again on a seasonal basis. Control of this pattern is probably dominated by temperature, although other factors such as resistance, salinity and food undoubtedly play a role.

Some experimental oysters survived with MSX for at least 4 years after they had acquired the parasite. These oysters were in poor condition, however, underscoring the imbalance of the host-parasite relationship and suggesting that chronically infected individuals, even though they are surviving with the parasite burden, would be less able to withstand additional stresses.

The influence of chronic infections on the MSX cycle in Delaware Bay is discussed.

GROWTH OF CLAMS *(MERCENARIA MERCENARIA)* IN GREAT SOUTH BAY, NEW YORK

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The natural beds of hard clams in Great South Bay support the most valuable hard clam fishery in the world. Despite the importance of the fishery, basic scientific knowledge of the population dynamics of the resource needed to effectively manage its utilization is lacking. The purpose of this research was to provide information on growth of clams in the Bay. The specific objectives of the research were to develop methods of determining growth rates, to determine the amount of time needed for clams to grow to harvestable size, and to determine how this time varied between different locations in the Bay.

Growth rates were determined through a combination of three methods: analysis of shell growth structure of individual clams, analysis of size frequency distributions of clam populations, and planting-recovery experiments. Natural stocks of clams at 15 locations in the Bay were sampled so that a variety of Bay environments would be represented. Incremental shell growth patterns of individual clams were studied to provide mean age-length relationships for particular year classes of clams at 10 stations. Analysis of year class peaks in size frequency distributions was performed to determine the size differential of clams from successive annual sets and growth rates of yearly sets. Planting and recovery of marked clams provided a direct measure of growth over an approximately one year period.

For all clams examined, growth rates were highest in the spring and fall. Reductions in growth occurred during the summer and winter apparently in response to unfavorable environmental conditions. Seasonal effects on growth were most pronounced in clams sampled from very shallow waters. Significant variations in growth rates were found in clams from different stations. Growth rates were greatest for clams from stations with well circulated waters and sandy sediments. Growth rates were lowest for clams from stations with silty sediments near river mouths. The maximum sizes reached by clams also varied greatly throughout the Bay. At some stations clams blunted and essentially stopped growing at the age of 5 or 6 years and length of 60 to 70 mm. Clams at other stations did not blunt until age 8 or 9 and length of 90 to 100 mm. In most areas examined, the majority of clams reached legal harvestable size (1 in. in thickness or 48 mm in shell length) after 3 to 3 1/2 years of growth. Some clams, however, required as little as 2 1/2 years and as much as 4 1/2 years to reach

harvestable size. Information on growth rates will be valuable to mangement programs designed to maintain the productivity of the hard clam resources of the Bay.

RECENT STUDIES OF THE SURF CLAM POPULATIONS IN SOUTHERN NEW JERSEY

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In earlier reports covering studies of the surf clam populations within southern New Jersey waters since 1972, the steady decline in standing stocks under generally increasing harvest pressure has been emphasized. Evidence for general setting and early growth of juveniles at densities averaging up to 300-400 per square meter has been presented, although survival of these juveniles beyond their first season has been low. In 1977 the population inventory, for the first time since 1972, produced evidence for significant survival of juveniles of the preceding year class (1976).

Results of standing stock inventories, size frequency studies and studies of juvenile mortalities and larval distribution will be summarized.

THE DISTRIBUTION OF OYSTER ROCKS IN THE RAPPAHANNOCK RIVER, VIRGINIA

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The Virginia Institute of Marine Science is charting the location of the natural oyster rocks on most of Virginia's 243,000 areas of public bottom.

In charting these natural rocks, stations are located with an electronic positioning system (Teledyne-Hastings-Raydist). At each station along series of transects, data relating to bottom type and depth is recorded. An underwater microphone towed astern of the research vessel gives information relating to the distribution of shell material.

Charts have been prepared showing the location, shape and size of the natural rocks in the Rappahannock River. This information shows that only about 33% of the public bottoms in that estuary are productive or potentially productive.

THE FOURTH FOLD AND SECRETORY RIDGE OF THE MANTLE EDGE OF THE LITTLENECK CLAM, *PROTOTHACA STAMINEA*

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The mantle edge of the littleneck clam, *Protothaca staminea*, is divided into four well-defined tentacular folds and a large glandular ridge dorsad to the fourth fold. The fourth fold is relatively large and is comprised primarily of mucocytes, while the secretory ridge contains a variety of mucopolysaccharide- and protein-secreting cells. The degree of development of the fourth fold in *Protothaca staminea* is equal to that described for the quahogs, *Mercenaria mercenaria* and *Mercenaria campechiensis*, and considerably greater than that described for certain other veneraceans. The embryological origin of the fourth fold within the veneraceans has yet to be determined, as does the function of this complex group of tissues.

OYSTER CULTURE IN WASHINGTON — PROBLEMS OF SHIFTING TO DOMESTICALLY PRODUCED SEED

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Over the past ten years there has been a decline in the production of oysters in the State of Washington. Reduced profitability of oyster culture has resulted in fewer acres of oyster ground being used. Since the cost of oyster seed amounts to 20% of the gross receipts from oyster

harvest, modest improvements in the productivity of seed could significantly improve profit margins. Traditionally, Pacific oyster seed has been imported from Japan. During the last decade, however, increasing reliance has been placed on domestic sources of oyster seed — wild seed, primarily from Dabob Bay on Hood Canal, and seed from several Pacific coast oyster hatcheries. Domestic seed generally costs less than an equivalent quantity of Japanese seed, but has the reputation of producing lower yields.

In 1975, lots of seed were obtained from Japan, Dabob Bay, and a hatchery. Experimental plots were established in three locations in Washington. Periodic measurements were made of seed growth and mortality over a two-year period. At termination, the number of gallons of oyster meat from each group was determined. Results showed that under comparatively adverse conditions, Japanese seed could be expected to produce higher yields. However, yield from domestic seed could be substantially improved by minimal efforts to protect it from certain mortality-causing factors. There were also indications that Japanese seed was more susceptable to the Puget Sound adult summer mortality syndrome.

A STUDY OF VIBRIOSIS AT A LONG ISLAND SHELLFISH HATCHERY

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A five year study (1973-1977) of the quantitative and qualitative bacterial flora of incoming bay and well water, stock and pooled algal cultures, and oyster larval curtures of a Long Island oyster hatchery located in the town of Oyster Bay was conducted. In addition, water quality studies were made of incoming hatchery bay and well water, taken at the time of bacteriologic sampling during a 3-year period (1975-1977). The relationship of *Vibrio* spp. isolated, to other bacterial isolates and water quality changes is the subject of this report.

Although *Vibrio* spp. were isolated at low frequencies throughout the shellfish growing season, they were found to be the dominant bacterial population in incoming bay water during a single peak period of each year. This peak *Vibrio* period was of variable duration and occurred in the spring or summer. A sharp drop in the ammonia levels of incoming bay water was noted during these peak *Vibrio* periods. The onset of this period was also associated with an increase in total bacterial counts and suspended organic content of the incoming bay water. Although such peak *Vibrio* periods occurred annually in incoming bay water, outbreaks of hatchery vibriosis, with high oyster larval morbidity and mortality, did not occur each year. When outbreaks did occur, they were first noted during the peak periods of *Vibrio* abundance in the incoming hatchery bay water supply. *Vibrio* spp. were isolated as the dominant bacterial population in successfully cultured hatches of oyster larvae and algal cultures during the course of continued hatchery infection. Although hatchery vibriosis was initiated during peak concentrations of *Vibrio* spp. in incoming bay water, the disease persisted in the hatchery after peak periods had passed, and *Vibrio* spp. could not be demonstrated in the incoming water supply.

The possible practical implications of these findings in the prevention, control and eradication of hatchery vibriosis is discussed.

*This research was sponsored by the New York Sea Grant Institute under a grant from the Office of Sea Grant, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce.

ABNORMALITIES IN THE SHELL OF THE MAINE-GROWN EUROPEAN OYSTER *(OSTREA EDULIS)**

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High percentages of the European flat oyster, *Ostrea edulis*, exhibit unusual greenish deposits on the inner valve surfaces. These deposits are conchyolinous in nature and differ from the blister typical of parasitic responses, in that they are firmly incorporated into the underlying shell

layer. A frequency study carried on at six commercial oyster grow-out sites along the coast of Maine, revealed variations in incidence attributed to site and age class. The percent occurrence at colder, northern sites was considerably less (14-34%) than at more southern, estuarine sites (16-80%), while older age classes exhibited higher frequencies (26-78%). Significant differences were also evident in percent coverage and areas of concentration on the shell surface. 86.5% of the affected oysters (470) had less than 20% of their valve surfaces covered, and the deposits were strongly concentrated on and around the adductor muscle scar and less significantly, in the hinge area.

The condition of the animals is unaffected and the mantle adjacent to the deposits appears to be unaltered. Histologic examinations have not yet revealed any possible etiological agents, although typical inflammatory responses are present in the tissues. SEM studies are presently underway to further describe the abnormal deposits, as well as continued histological and decalicified shell smear preparations. Speculations are made on the etiology of the abnormal deposits, both from a pathological and an environmental viewpoint.

*Winner of Thurlow C. Nelson award as outstanding paper by a junior scientist.

THE BIVALVE "LARVAL LIGAMENT PIT" AS AN EXCLUSIVELY POST-LARVAL FEATURE

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Laboratory culture experiments, coupled with detailed examination of published micrographs, have provided evidence that morphological structures of bivalves heretofore referred to as "larval ligament pits" are post-larval features. Results further suggest that careful examination of the ventral surface of the hinge apparatus of the shells of small planktic bivalves provides a means of ascertaining whether or not the process of metamorphosis has been initiated. The presence of a ligament pit in such shells indicates that attachment (or at least byssal secretion) has occurred, while the size and development of this structure is of assistance in determining the extent to which the process has proceeded. If, as has been suggested by Bayne (1965), secretion of the dissoconch shell marks the end of metamorphosis, the prodissoconch-dissoconch boundary provides a morphological feature useful in distinguishing true juveniles from "metamorphosing" post-larvae. On a population level, comparison of temporal relationships between development of these two morphological shell features (ligament pit and prodissoconch-dissoconch boundary) should contribute much to our understanding of ecological factors affecting both settlement and metamorphosis of numerous Recent and fossil bivalves.

MICRO- AND ULTRAMORPHOLOGY OF LARVAL BIVALVE SHELLS: ECOLOGICAL, PALEOECOLOGICAL, AND PALEOCLIMATIC APPLICATIONS

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While the potential usefulness of larval bivalve shells in biological and paleontological studies has been emphasized by numerous authors, applied research efforts have been frustrated largely by an inability of workers to identify these specimens at specific, or even generic, levels using routine microscopic procedures. Results obtained over the past seven years have provided an important step towards elimination of many practical barriers and we here suggest a method whereby individual larval and early post-larval specimens of certain closely related species (both recent and fossil) may be differentiated through detailed examination of the hinge apparatus. In addition, planktotrophic and nonplanktotrophic forms are readily differentiated through detailed examination of the hinge apparatus. In addition, planktotrophic and nonplanktotrophic forms are readily differentiated through detailed examination of external larval shell morphology. The ability to distinguish and categorize (according to developmental type) such larval forms in coastal and oceanic waters should provide the groundwork necessary for

testing recent hypotheses concerning the importance of larval dispersal in maintaining genetic continuity between populations of marine species widely distributed along the continental margins or even isolated from each other by ocean basins.

The shell morphology of larval and early post-larval bivalves may also be of assistance in paleoclimatic studies. For those species which have been examined in detail, negative correlations have been found between temperature and maximum shell size at metamorphosis. To the extent that initiation of deposition of the dissoconch shell marks the end of metamorphosis, the prodissoconch-dissoconch boundary provides a morphological feature useful in distinguishing true juveniles from larval forms or metamorphosing post-larvae. Such boundaries are readily distinguished in specimens from sediments as old as the Late Cretaceous and, when coupled with size distribution data for larval specimens, can be used in defining maximum sizes at metamorphosis. Detailed examination of changes in the morphometry of this boundary in a species through time at a single locality, or in a series of localities along a single horizon, should provide an indication of temporal or spatial pileotemperature gradients. The long geologic duration of most bivalve species suggests that absolute paleotemperature estimates might be achieved for Early Holocene, Pleistocene, and Pliocene sediments using regressions of prodissoconch length on temperature for a variety of living species.

GROWTH AND SURVIVAL OF HATCHERY-REARED AND WILD OYSTER SPAT IN MISSISSIPPI SOUND AND ADJACENT WATERS

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The growth and survival rates of hatchery-reared spat are compared with those of wild spat at five locations in Mississippi Sound and adjacent waters. Oysters were marked, measured, and placed in trays at selected sites. Subsequent measurements were made each month for one year and mortalities were recorded.

Significant differences in growth rates exist between hatchery-reared and wild oyster spat at one location. In addition, comparisons between stations of either hatchery-reared or wild oyster spat show that growth rates are significantly higher at some stations than others. No significant differences in overall survival rates were found between the various locations.

CHALKY DEPOSITS IN THE SHELL OF *CRASSOSTREA VIRGINICA*: ULTRASTRUCTURE AND ENVIRONMENTAL INTERACTIONS

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Dead-white, porous chalky deposits may constitute nearly one-half of the shell of mature oysters (*Crassostrea virginica*), and are important determinants of shell strength, hardness, and density. Along with several other morphological and ultrastructural characters, chalky deposits were investigated as a possible indicator of growing conditions in three environments. These environments included Broadkill Creek, an excellent natural site for oyster growth, and two systems in the University of Delaware mariculture facility at Lewes; namely a "flow-through" and a "recycle" (closed) system. Spat from a single spawning were set into each of the three systems in fall, 1976, and summer, 1977, and morphological, mineralogical, ultrastructural, and chemical parameters monitored for 42 and 16 weeks, respectively.

An apparatus was developed which permitted shell volume measurements to be made with a precision of 0.01 cc. As a result, shell density, a reliable indicator of amount of chalky deposits, was determined with considerable accuracy. Shell density of oysters grown in "recycle" (2.81 ± 0.150) was significantly different from that of oysters grown in Broadkill Creek (2.29 ± 0.130) or "flow-through" (2.33 ± 0.115). Factors regulating amount of chalky deposition in oysters from the three systems may include growth rate and ambient calcium levels.

In these juvenile oysters, chalky deposits were normally located in a semi-circular band along the

prismatic-calcitostracum interface of the attached (left) valve. The thickness of the deposits was greatest along the anterior and posterior margins of the semicircle, All regions of the mantle capable of depositing calcitostracum can also deposit chalky shell, and in older oysters chalky deposits are more randomly distributed.

SEM indicated that units comprising chalky shell strongly resemble those of calcitostracum in size and shape. But, whereas the calcitostracal tablets are closely opposed in lamellae parallel to the inner shell surface, those in chalky shell form a porous, honeycombed structure and are oriented perpendicular and obliquely to the shell surface. It is not known whether chalky shell is deposited in a porous condition, or if it is formed by reorganization of calcitostracum. Scanning micrographs of the inner shell surface reveal a continuum of structures intermediate between calcitostracum and chalky.

EFFECTS OF TEMPERATURE AND SALINITY ON METAMORPHOSIS IN TWO TROPICAL MUSSELS

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Effects of temperature and salinity on the metamorphosis of tropical mussel larvae (*Perna perna* and *P. viridis*) were tested in a series of multivariate laboratory experiments. Between 10 and 12 days after fertilization, larvae of both species secreted byssal threads for the first time denoting the onset of metamorphosis. Time to the onset of metamorphosis was relatively independent of salinity. Within a broad range of temperatures, time to onset of metamorphosis was more a function of time than of growth rate. Metamorphosis occurred only at temperatures between 18°and 30°C. At lethal and sub-optimal temperature and salinity combinations, increased mortalities were associated with the onset of metamorphosis. Pre-metamorphic mortalities were not observed in cultures reared at near optimum conditions. Greatly diminished feeding rates (cells/larva/hour) immediately preceed these mortalities. Because larvae completing metamorphosis resorb the velum and then cease feeding, I propose that temperature and salinity stress forced immediate completion of metamorphosis. Delayed metamorphosis was not favored at lethal or sub-optimal temperatures or salinities. Pre-metamorphic mortalities result from the larvae's inability to feed while continuing to search for a suitable substrate for settlement.

Compared to other temperature and salinity responses of these larvae, the duration of the delay in metamorphosis was restricted to relatively few temperature and salinity combinations. Optimum conditions for delaying the completion of metamorphosis are similar to those resulting in highest growth rates.

Larvae held at sub-optimal temperatures and salinities during their early pelagic development were still able to metamorphose. Unless suitable substrates for settlement are available precisely at the onset of metamorphosis, these stressed larvae will suffer increased mortalities and provide little recruitment to mussel beds. Larvae living at near optimum conditions at the onset of metamorphosis are able to delay the completion of this critical stage, increasing the probability of locating a substrate for primary settlement. Thus survival and subsequent recruitment are dependent more on the environmental conditions experienced during and after metamorphosis than on the conditions under which the early larval stages developed.

A PRELIMINARY REPORT ON THE NORMAL HISTOLOGY OF THE DUNGENESS CRAB, *CANCER MAGISTER*

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The published literature contains virtually no information on the normal histology of the Dungeness crab, *Cancer magister*. Indeed, the internal gross anatomy is largely undescribed. Therefore, it has been necessary to study the normal histology of the animal prior to initiating investigations of the reaction to injury and wound repair processes, rate and pattern of post mortem

changes, and the pathological effects of infectious and non-infectious diseases.

This is a preliminary report on the structure, but not the function, of a number of organs of the Dungeness crab. These include the gills, heart and hemopoetic tissue, gastro-intestinal tract, bladder, epidermis, ovary and testis, and brain and thoracic ganglion.

ABSTRACTS OF INVITED PAPERS NOT APPEARING IN THIS ISSUE

PASTEURIZATION OF OYSTERS

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The development of a lightly heat-treated in-shell oyster product that can be utilized as an adjunct to the raw oyster is presented. Method of preparation, shelf life, organoleptic properties, microbiological and chemical aspects as well as economics parameters for production are discussed. The data includes yield information relating to time and temperature of steaming, texture determination with a sheer press as well as taste panel evaluation. Cost analysis for current equipment is also included.

THE CULTURE OF ABALONE

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In the Pacific Basin countries of Japan, China, Korea, Australia, New Zealand, Mexico and the United States, various species of abalone (family Haliotidae; class gastropoda) are of significant commercial importance. In California the abalone foot is prepared as steaks and sold as a premium restaurant item. In the Orient abalone is consumed in a wide variety of forms, including raw, in soups, and in vegetable dishes. The demand for abalone has increased in recent years and the supply has dramatically decreased, thereby providing an incentive for developing abalone culturing technology.

Culturing technology in Japan and the United States has developed and mariculture production is undergoing considerable expansion. The culturing of abalone involves eight separate stages of growth, with distinctly different culturing requirements. The experiences gained from pioneering abalone culture should be of value in developing mariculture technology for other species.

The development of abalone culturing technology has involved understanding and controlling diseases, environmental factors and nutrition; the application of such scientific knowledge into engineered systems; and most recently, genetics. Some eleven identifiable scientific and engineering disciplines have been utilized.

CLIMATOLOGICAL EFFECTS ON DISTRIBUTION CATCH AND ABUNDANCE OF THE BLUE CRAB

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Large fluctuations in the Chesapeake Bay blue crab catch have occurred over the last 100 years. Abundance and distribution are believed to be dependent largely on environmental factors, such as temperature, salinity, dissolved oxygen, predation, disease and food supply. Spawning stocks are believed to have been adequate to maintain the population.

The Chesapeake Bay is an area of large seasonal and annual environmental changes, in particular in temperature and in rainfall and consequent runoff. An attempt is made to describe in broad terms, the natural environmental boundaries of spawning grounds and nursery grounds, the theoretical displacement of these grounds in extremely wet and dry seasons, and to explore the influence these variations have on yearclass strength of the blue crab.

PAPERS READ BY TITLE

A COMPREHENSIVE SURVEY OF SOUTH CAROLINA'S HARD CLAM RESOURCES

William D. Anderson, Willis J. Keith, F. Holland Mills, Michael E. Bailey, and John L. Steinmeyer

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Hydraulic patent tongs were used in a comprehensive resource survey to inventory South Carolina's hard clam standing crop. During the four year survey (1973-1977), 35,922 square yard (0.84m^2) bottom samples were taken throughout the state's estuaries to assess clam densities and bottom types. An estimated 6,809 acres (2,756 ha) of clam bottoms were found in contagious distributions. Seventy-eight percent of the total clams sampled and highest clam densities were found co-incident with a mixture of shell and sand substrate. Initial survey results during the fall of 1973 and early 1974 resulted in the discovery of high density subtidal clam populations in the Santee River estuary. Based on these sampling results and the interest of clam fishermen, hydraulic escalator harvesters were introduced into the Santee estuary and the fishery has continued to the present time. Seven permits are issued annually and harvesting is managed by the Division of Marine Resources. Since the 1974-75 clam season, South Carolina's hard clam ex-vessel revenue has exceeded the pre-survey annual average production level by six times.

SOUTH CAROLINA'S FIRST CALICO SCALLOP FISHERY

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On June 15, 1977, high densities of calico scallops (*Argopecten gibbus*) were found approximately 60 miles offshore of the South Carolina-Georgia border at depths of 37 to 45 meters. Mean shell height from four locations on the bed ranged from 26.4 mm to 31.4 mm. Monthly growth measurements in conjunction with a resource assessment to determine the extent of the scallop community showed expotential shell growth ($r^2 = .9781$) through the November 8, 1977 ($\bar{x} = 48.5$ mm) survey. Meat yield at this time was commercially favorable and the scallops shucked out to approximately 960 meats per gallon. Local commercial shrimp fishermen were advised of the resource potential in November, but were reluctant to invest in scallop fishing gear at this time. However, in early January, seven Florida scallop trawlers began harvesting the bed and meat yields ranged from 1200 to 650 per gallon. Successful prosecution by Florida boats caused local fishermen and several from North Carolina to enter the fishery. In mid-January, 1978, the R/V DAN MOORE from the North Carolina Division of Marine Fisheries surveyed the scallop bed and determined its area to be approximately 35 square miles, elliptically shaped and perpendicular to the coast. Density and meat yields decreased from inshore to offshore areas. By March, approximately 45 vessels from Florida, North Carolina and South Carolina were actively harvesting scallops and an average meat yield of 504 meats per gallon was recorded in the most productive bed area on March 7, 1978. Although the scallops were landed at three South Carolina ports, they were processed and marketed in Florida and North Carolina. At the end of March, over $800,000 in ex-vessel scallop revenues had been landed in South Carolina.

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ABSTRACTS OF TECHNICAL PAPERS PRESENTED AT NSA WEST COAST SECTION MEETING

BIOCHEMICAL CHANGES IN THE PACIFIC OYSTER, *CRASSOSTREA GIGAS* (THUNBERG, 1795) DURING LARVAL DEVELOPMENT AND METAMORPHOSIS

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The energy strategies of early development of the Pacific Oyster, *Crassostrea gigas*, were examined. Changes in proteins, total carbohydrates, free reducing sugars and total and neutral lipids were determined for the unfertilized egg and larval stages through 13 days post-settlement. Micro-analytical methods were employed in the fractionation and end product analysis of 5-10 mg freeze-dried whole eggs, larvae and spat.

During early larval stages neutral lipid levels decreased and provided the principle source of energy for development (21-10% of the total organic matter). Subsequently they remained unchanged throughout settlement and metamorphosis.

Protein levels increased during larval stages (65-80% of the total organic matter) and remained largely unchanged after settlement. Total carbohydrate levels were unchanged during larval development and through settlement and metamorphosis (2.5% of the total organic matter). Phospholipid values rose slightly (6-10% of the total organic matter) during early larval stages and remained unchanged through settlement and metamorphosis.

Starvation experiments confirmed the aforementioned findings that neutral lipid provided the principle source of energy during early larval life (0.151 cal/larva/day for neutral lipid and 0.107 cal/larva/day for protein). Protein, however, contributed more energy than neutral lipid in late larval life (2.26 cal/larva/day for protein and 1.09 cal/larva/day for neutral lipid).

The literature states that planktotrophic bivalves accumulate neutral lipid during larval feeding as an energy store to be drawn upon during the nonfeeding period of settlement and metamorphosis. This study has shown that in *C. gigas* development neutral lipid was not accumulated during larval feeding nor utilized during settlement and metamorphosis relative to other organic fractions. This contradiction in energy strategy suggests the need for more information on the patterns of energy storage and utilization in planktotrophic development.

EYED LARVAE AND THE OYSTER GROWER

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A new method of seed production from hatcheries involve the eyed larvae technique. With this method, advanced or eyed larvae are filtered from the rearing tank and wrapped in a damp cloth surrounded by wet paper towels. They are then transported in a styrofoam chest by car or air. Upon receipt by the grower the larvae are put into enclosed seawater with the cultch (shell, chips, etc.). Within twenty-four hours (usually less than twelve) the larvae are set. The cultch with the spat should be put directly into the bay.

Usually about twenty percent of the larvae set. Larvae have been kept in the damp state under refrigeration for seven days and still set. This is not recommended. Larvae should not be held more than forty-eight hours in the damp state.

There is now one commercial hatchery producing eyed larvae and several growers utilizing them. Conditions for set: bay water, usually filtered but not always, temperature 18°C or above, should have some provision for heating water, clean cultch and as soon as the larvae are set get them into the bay.

THE DEVELOPMENT OF A MANAGEMENT PLAN FOR A CLAM FARM IN SOUTH PUGET SOUND, WASHINGTON

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A management program is being developed for a clam farm in Little Skookum Inlet on Puget Sound. A series of inventories of the Manila clam (*Venerupis japonica*) resources has been taken, and estimates of standing stock, age distribution, and growth have been determined. Methods to determine the basic physical and environmental factors at work include an aerial photographic record of the changes in the tideflats, systematic monitoring of the clam population, and detailed mapping of the clam beds with respect to substrate and clam densities. The authors hope to determine currents, substrate and other factors that influence the setting and distribution patterns of Manila clams at this site.

THE RELATIONSHIP BETWEEN *MYTILUS EDULIS* LARVAE IN THE PLANKTON AND SETTLEMENT IN HOLMES HARBOR, WASHINGTON

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Obtaining a settlement of larvae has been an obstacle to mussel culture in parts of Puget Sound. To investigate factors that could be used as indicators of settlement time a quantitative study of the occurrence of *Mytilus edulis* larvae in the plankton was performed at Holmes Harbor, Washington, from autumn through spring (1977-78). Plankton samples were taken using a pipe and pump operated from a moving boat. Larval settlement was monitored using rubberized curled hair packing material as a settlement substrate.

A synchronous mass spawning during the second week of April was described by the number of larvae in the plankton. After the mass spawning the number of larvae fluctuated with a bimonthly periodicity. The periodicity may have resulted from a tidal spawning rhythm and/or tidal transport of larvae. Larvae from the spring spawning reached peak settlement at the end of May. The duration of the planktonic existence was estimated to be 5 to 7 weeks.

For predicting settlement time the increase in larval abundance with the onset of the spawning season would be useful. Also, a correlation between the proportion of mature larvae in the plankton and settlement of larvae was found. The results indicate that the number of eyed larvae is correlated to the number of settled larvae and might be the easiest predictive measure to use. Larval settlement should not be a limiting factor to a mussel culture industry in Holmes Harbor.

POTENTIAL FOR MUSSEL CULTURE IN BUDD INLET, WASHINGTON

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There exists the potential for a substantial mussel aquaculture industry in Puget Sound. There is a need to identify seeding and growing areas within the Sound. Budd Inlet is one of the shallow finger bays at the southern end of the Sound that is artifically enriched by the City of Olympia.

The Department of Natural Resources has been using synclove rope, polypropylene rope and plankton tows to monitor timing of the mussel sets in Budd Inlet since 1975. Massive setting occurred in June 1975 and in May 1976, 77 and 78. In

March, 1978, the Department of Fisheries established 10 mussel spat collecting stations scattered throughout Puget Sound. The spat collectors consisted of 10 x 20 cm x 2" blocks of rubberized hogs hair. The collectors were changed at approximately two week intervals. Budd Inlet had the highest concentration of mussels with 64,000 having set on the collector between April 25 and May 11. Setting continued at a reduced rate until July when the count dropped below 160 spat. Six out of the 10 stations in Puget Sound had counts that were over 100 mussels each. With the exception of Totten Inlet, also in south Puget Sound, all of the remaining sets were later in the summer. Penn Cove on Whidbey Island was the only area where the numbers approached those of Budd Inlet with sets of 2500 to 3300 occurring in late May and June.

On June 29, approximately one month after setting, we counted the set on a 120 cm long 3/4" synclove rope. We counted 10 cm sections spaced at 1/2 meter intervals. The count was as follows: surface 160 mussels averaging 3.1 mm; at 1/2 meter, 993 mussels averaging 4.1 mm; at 1 meter 1006 mussels averaging 3.6 mm; at 1½ meters 475 mussels averaging 3 mm; at 2 meters 388 mussels averaging 2.5 mm; at 2½ meters 480 mussels averaging 1.9 mm and at 3 meters 255 mussels averaging 1.6 mm. The estimated total for the rope was 16,400 mussels. Fish grazing could have removed the larger mussels from the lower sections of rope. Polypropylene rope appeared to catch seed equally well.

The mussel growth rate is good in Budd Inlet. Mussels set in late May average 27 mm by October, 40 mm by March and 47 mm be June 1. Some 43% by number and 61% by weight of these one year old mussels were above the 50 mm commercial size.

On the negative side, the pile perch and shiner perch prove to be very serious predators. These fish eat virtually all of the mussels below the first meter on ropes that are not protected by netting. White wing and surf scoters and Barrow's goldeneye feed very heavily on the mussels during the fall and winter. Fouling with barnacles, mussels, bryozoans and anaerobic conditions caused by poor circulation become very bad after March 15. Ropes of mussels weighed and measured June 1, 1978 contained 18% dead shells. There were almost no dead shells in the samples taken on March 29. The cause of this mortality is as yet unknown.

In summary, Budd Inlet is a very good place to catch spat and study mussel problems.

EVALUATION OF CLAM RESOURCES OF THE S. E. BERING SEA

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During the past 3 years, the National Marine Fisheries Service in cooperation with the State of Alaska and several sponsoring private companies surveyed the S. E. Bering Sea to determine the commercial potential for sub-tidal clams. The research in 1977 and 1978 included sampling with hydraulic harvesters. The 1977 survey defined 1,600 square miles north of the Alaska Peninsula where clams were available in sufficient quantity to warrant further study. The 1978 research concentrated in areas where it appeared commercial quantities of clams might be harvested.

Clams with potential for utilization include the Alaska surf clam (*Spisula polynyma*) and the Great Alaskan tellin (*Tellina lutea*). The 1977 survey resulted in discovery of an estimated 286,184 metric-ton, surf-clam resource.

Samples of the clam catches taken from depths between 5 and 28 fathoms were analyzed for paralytic shellfish poison (PSP). In 1977, no detectable PSP was found in the surf clam. The tellins in 14 of 22 areas checked had PSP in the visceral portions. In 1978, the PSP analyses show that both surf clams and tellins in some areas do have detectable PSP in the meats and the viscera. Although the PSP problem does not appear to be great, it does indicate the need for a monitoring program in order to utilize the resource.

THE DETERMINATION OF CELLULASES IN THE GIANT MALAYSIAN PRAWN, *MACROBRACHIUM ROSENBERGII* (DE MAN)

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One of the critical factors in the cost of the commercial production of the giant Malaysian prawn, *Macrobrachium rosenbergii* (de Man), is the cost of feeding juvenile prawns in the grow-out ponds. A possible way to reduce this cost is through the use of a cheaper protein/carbohydrate/fat mixture by increasing the amounts of the carbohydrate, in the form of cellulose, and decreasing the amounts of protein. The first step in this direction is to determine the presence of cellulases, the enzymes necessary to break down cellulose.

Cellulolytic activity in the Malaysian prawn was examined via the use of the Somogyi-Nelson assay method for reducing sugars. The gastrointestinal tract with its contents intact, the stomach, the intestine, and the hepatopancreas, as well as the solid contents and filtrate from the solid contents of the stomach were examined for activity. Samples from homogenates of the organs, the solid contents, and the filtrate were incubated with a cellulose powder suspension as a substrate.

Activity was found in the homogenate of the gastrointestinal tract with its contents intact, and in homogenates of the stomach, the intestine, the hepatopancreas, and the solid contents and the filtrate of the contents. Mean reducing sugar levels indicate greater cellulase production occurring in the organs rather than in the gut contents.

THE SPATIAL OCCURRENCE OF THE CLADOCERAN *MOINA MACROCOPA* IN A KRAFT PULP MILL TREATMENT LAGOON[1]

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Adequate waste treatment and recycling are important targets for pollution abatement. Biological treatment is accomplished by uptake and conversion of inorganic nutrients by primary producers and, to a lesser degree, by cell wasting and the consumption of primary producers by zooplankton. This study is a survey of *internal* waste treatment occurring in a pulp mill lagoon emphasizing the role and utilization of a major inhabitant species, the cladoceran *Moina macrocopa*.

It was found through feeding studies in the laboratory that *Moina* decreased TSS (total suspended solids) 3.5% to 34% over control groups in Weyerhaeuser's Everett Kraft effluent. To determine if this added reduction took place under field conditions, a one-year study of the pond's physical and biological parameters was undertaken. By grouping data based on the presence or absence of *Moina*, T-test analysis was performed comparing group means for TSS and BOD (bio- chemical oxygen demand). When *Moina* were present TSS and BOD group means were significantly lower than when the cladocerans were absent. Multiple regression analysis showed that 31% of the observed variation of *Moina macrocopa* populations in the field could be accounted for by TSS, BOD, pH, temperature, sunshine, and dissolved oxygen.

Moina macrocopa collected from the Everett Kraft Biopond were nutritionally analyzed resulting in the following: 70% crude protein, 10% fat, 8% ash. Utilization of these cladocerans as a potential fish food was initiated by feeding them to rainbow trout, *Salmo gairdneri*. No mortality or statistical difference in growth was apparent between *Moina* fed and control (Clark and Moore) group.

A marketing survey based on utilization of *Moina macrocopa* as a tropical fish food was conducted with encouraging results. Various methods of mass harvest of *Moina* were evaluated with regard to labor, expense, and catch attained. Wholesale prices of frozen cladocerans were estimated to be in the range of $.50 to $3.00 per pound (depending upon handling procedures),

while retail values ranged from $5.00 to $15.00 per pound. It was found that *Moina* were harvestable in commercial quantities, with demonstratable demand as a market item.

Thus, *Moina macrocopa* in a Kraft pulp mill lagoon enhanced waste treatment as well as demonstrated the potential value of a recycled waste by-product.

[1]This project was jointly funded by the Weyerhaeuser Company and the Washington Water Research Center.

HOW DO YOU KEEP AN OYSTER DOWN ON THE FARM: OR RECENT DEVELOPMENTS IN THE BRITISH COLUMBIA OYSTER INDUSTRY

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The Pacific oyster industry in British Columbia, at its beginning, was an intensive culture operation, that is bringing oyster seed from external sources to the growing areas to culture to maturity. A massive spatfall in 1958, in the Strait of Georgia, established the present "wild" range of the species, and by 1963, changed the oyster industry from a cultural operation, to basically a fishery.

In recent years, the lack of significant recruitment, combined with increasing recreational pressure on the wild oyster resource, has brought about a large decline in the once abundant stocks. Commercial harvesting is now severely restricted forcing the oyster industry to again adopt the "farming techniques" which were practiced in the past.

The most significant increase in oyster culture activity has been in the area of seed collection. New people are involved in this segment of the industry, the amount of cultching is increasing, a variety of methods are being employed, and government regulations and policy has been enacted to further encourage the industry.

COMPARISON OF SEVEN TYPES OF OYSTERS GROWN IN YAQUINA BAY, OREGON, FROM AN OYSTER FARMER'S POINT OF VIEW

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This presentation is a totally practical but non-scientific comparison of seven oysters rated in ten categories. The native Yaquina oyster (*Ostrea lurida*) is the worst commercial oyster for many reasons such as low survival rate, slowest growth, high production cost, and low commercial demand. The European oyster (*Ostrea edulis*), having the same characteristics and drawbacks (except a larger maximum growth size), is no better. The Eastern oyster (*Crassostrea virginica*) is basically a loser for our purposes, since it has many of the same characteristics as the common Pacific oyster (*Crassostrea gigas*), but to a lesser degree of quality. For example, they grow longer, thinner, and with less meat. The common Pacific oyster is still the main source of our business since it is extremely hardy and also flexible in grow-out methods and marketing. The seed is comparatively easy and cheap to buy, does very well as a cocktail oyster for six to eight months of the year, is in high demand fresh in the shell, and grows fast for use as a larger oyster. The Kumamoto variety is irreplaceable and unsurpassed as a cocktail and halfshell oyster. Growing no longer than petite size, the flavor, texture, and cooking characteristics make this oyster appealing even to those who dislike the Pacific oyster. Being in season all year ensures a steady business for the oyster grower. However, it is impossible to buy the seed. The Gigamoto variety, being a half-breed, seems to have equal characteristics of both. Being very easy to produce seed in the hatchery makes this oyster very promising for the future. The Sumino oyster is also very promising, except for cocktail and fresh shellstock use. The 50% faster growth rate than Gigas, its being in season all year, its nice flavor, and easy hatchery production makes this oyster most promising. At this time, seed is not available.

GROWTH AND SURVIVAL IN NEWLY SETTLED SPAT OF THE MANILA CLAM, *TAPES JAPONICA*

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Substrate abundances of adult Manila clams were manipulated in July 1976 on a portion of a beach dug commercially in the southern region of Puget Sound, Washington. Differences in clam spat growth and survival were measured between samples taken from substrates having varying levels of adult clam abundances.

The clam spat settled at densities ranging from 17,000 in substrates with high adult clam abundances to 31,000 in substrates with no adult clams. The clam spat settled at 0.206 mm in length. For clams that settled in July, the first growth ring occurred three months later, in October, at a length of approximately 5-8 mm. Clams that settled in September did not reach 5-8 mm in length until the following July, and attained their first visible growth checkmark the following October at a length of approximately 14-16 mm. Growth was significantly less in treatments with high adult clam densities. The density of small clams in June was approximately 1.2% of the initial settling density, and by June no difference in survival rates was detectable between clams from substrates with or without adult clam abundances.

Clam spat movement was detected on the beach. This may have contributed to the high spat mortality rate.

INFORMATION FOR CONTRIBUTORS TO THE PROCEEDINGS OF THE NATIONAL SHELLFISHERIES ASSOCIATION

Original papers given at the Annual Association Convention and other papers on shellfish biology or related subjects will be considered for publication. Manuscripts will be judged by the Editorial Committee or by other competent reviewers on the basis of originality, contents, clarity of presentation and interpretations. Each paper should be carefully prepared in the style followed in the 1972 PROCEEDINGS (Volume 63) before submission to the Editorial Committee. Papers published or to be published in other journals are not acceptable.

Manuscripts should be typewritten and double spaced; original and two copies are required to facilitate reviews. Tables, numbered in arabic, should be on separate pages with the title at the top. Scientific names should be underlined. Illustrations preferably should be 8 x 10 inch prints which can be reduced to a size of 6¼ x 8 inches or smaller. Glossy photographs are preferred to originals. Illustrations smaller than a page should be carefully oriented and loosely attached to plain white paper with rubber cement. Legends should be typed on separate sheets and numbered in arabic.

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PAPERS INVITED TO BE PRESENTED AT 1978 NSA ANNUAL MEETING

PROCEEDINGS
OF THE
NATIONAL
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