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Cover

Pearls in the blue mussel, *Mytilus edulis*.

Photo by R. A. Lutz (See page 17).

FURTHER NOTES ON HOW OYSTERS LAND WHEN PLANTED¹

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ABSTRACT

Woodward, Huxley and Moebius saw that oysters always set on the left valve. Later Stafford, Prytherch and Ranson observed cementation by the left prodissoconch (larval shell). However Cunningham and Orton stated that *Ostrea edulis* often come to lie on the right valve. Apparently this is of little consequence on hard bottom, but in mud the situation is considered to be harmful for reasons summarized by Needler. Gunter and McGraw found that oysters culled from clumps landed upside down when planted in water 59% of the time. This is attributed to poor shape of the oysters.

Natural single oysters numbering 1,423, which had been dredged from wild reefs, were selected or culled to singles and shovelled overboard into fresh water 1.5 to 3 meters deep. Oysters were seen to stabilize in about the first half meter when thrown into the water and then fall unchanged, upside down or not, to the bottom.

Out of 4,269 shovel-tosses of the 1,423 oysters (3 each) 2,447 (57%) landed on the left valve and 1,822 (43%) landed on the right valve. In three replications of the experiment the preponderance of the total sample came to rest normally on the left or lower valve, and of the total 488 individuals (34%) consistently settled normally whereas only 108 individuals regularly came to rest on the dextral valve.

INTRODUCTION AND REVIEW

In an attempt to analyze some of the aspects of oyster culture a little closer, the writers have continued work on how single oysters land on the bottom when thrown overboard. This appears to be a simple and overly pedestrian matter but it has an interesting history in the literature, with some examples of how disagreements and misunderstandings can occur over simple matters.

The early conchologists showed that the oysters come to rest on the left or convex valve by attachment (Cf. Woodward 1878), and generally lie that way, contrary to *Anomia* and *Pecten* which rest on the right valve. Nevertheless, Cunningham (1885) of the Scottish Marine Station disputed this view and said that most oysters in the Firth of

Forth rest on the right valve and are heavily fouled only on the upper (left) valve. This was quickly disputed by Hunt (1885), who said that all oysters attach by their convex (left) valves as stated by Woodward, Jeffrey and Huxley. Moebius (1885) quickly affirmed that oysters set with the nucleus of the left valve attached to the substrate. It is now well known through the observations of Huxley (1883), Stafford (1910) and Prytherch (1934) that the larvae always cement the left valve down. The "nucleus" of Moebius is the left valve of the prodissoconch or late larval shell stage, which Ranson, (1960) found attached even in fossil oysters. Thus, how oysters set and how they come to lie on the bottom became confused, at least in the minds of some people.

And so it would appear that the natural position of oysters was well settled years ago. Even so, modern workers have caused further discussion

¹ Presented at 1976 Annual Meeting of the National Shellfisheries Association.

and according to Orton (1937, p. 14), "In life the flat or right valve usually rests on the sea-bottom and is often referred to as the lower one." This caused Galtsoff (1964, p. 16) to say that "Orton's (1937) statement...is an obvious oversight." But Galtsoff overlooked Orton's deferred explanation on p. 27 which says, "When oysters are thrown in the water they usually settle with the flat valve on top. In this position the shell is liable to be washed about by any water-current and eventually to topple over to rest on its flat side." In short Orton explains the observations of Cunningham (1885) while verifying the general ideas and observations of zoologists concerning setting on the left valve.

With regard to the turning over of the European oyster, *Ostrea edulis* L., by currents as observed by Cunningham (1885) and Orton (1937), we call attention again to the observations of Emery (1908) on the same phenomenon regarding empty pelecypod shells on the continental shelf.

How Oysters Come to Lie When Planted in the Water

Orton (1937, p. 27) said merely in passing that when oysters are thrown into the water they usually settle with the flat (right) valve on top.

Needler (1938) applied himself to this question and came to several conclusions, some of which confirmed our observations independently, because we never acquired his paper until the last moment. They may be summarized as follows:

The normal position of an oyster on firm bottom is with the curved (left valve) down. On soft bottom they sink by the hinge end with the "lip" up. In upside down oysters the "lip" grows upward, producing distortion. For the best shape oysters should lie in the normal position.

Oysters smother more readily when upside down.

About 95% of well-shaped oysters landed right side up in water over three feet deep. The same percentage righted themselves within a foot or two when let in the water upside down.

Crooked oysters more often land upside down. Loose shells or other oysters caused oysters to turn over. Water helps in positioning oysters and it is better to plant with a tide than on bare ground.

Galtsoff (1964, p. 16) touched upon this question with his statement, "In *C. virginica* the left valve is almost always thicker and heavier than the right one. When oysters of this species are dumped from the deck of a boat and fall through water they come to rest on their left valves. I observed this many times while planting either small oysters not greater than 2 inches in height, or marketable adults of 5 to 6 inches."

Other authors seem to have used estimates. Gunter and McGraw (1974) seem to be the only workers who have presented quantitative data on this question. They found in Mississippi that wild reef oysters separated from clusters and culled into singles landed right side up only 41% of the time. However, the oysters used in these trials were essentially misshapen from having been grown together and lingering doubts over these results caused us to re-examine the situation. We might say here briefly and quickly that we have come to the conclusion that these results are an example of what Needler was talking about when he said, "Crooked oysters more often land upside down."

PRESENT WORK AND RESULTS

The writers carried on a further series of simple experiments using 1,423 oysters of which 937 were seed oysters under 50 mm in length. These were collected from natural reefs in Mississippi Sound by dredge and most of them were selected as singles, but some were culled. They were shovelled overboard into clear fresh water in swimming pools 1.5 to 3 meters in depth. Observation was then made by scuba diving and picking up all the oysters that landed right side up. Then the upside down oysters were collected and both sets counted. This whole process was repeated three times. The results are given in Table 1.

The departure of these results from a predictable norm based on mere chance is given in Table 2. Actually when this is calculated as the probability function of a binomial distribution, the chances that the type of distribution shown here would occur naturally intrinsically in a 50-50 distribution is less than one in a billion. Translated from statistical terms to the vernacular, this means that there is practically no chance that these results are matters of chance.

TABLE 1. Resting positions of 1423 "planted" oysters during each of three consecutive trials.

▼ = At rest on right valve
 ▲ = At rest on left valve

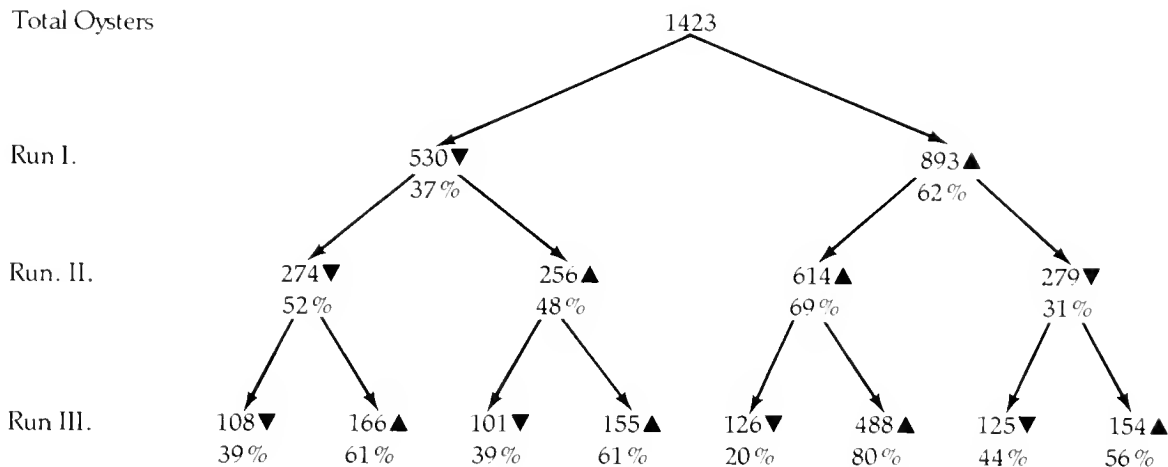


TABLE 2. Comparison of calculated and observed orientation of 1423 "planted" oysters.

	Dextral (On Right Valve)		Sinistral (On Left Valve)	
	Calculated	Observed	Calculated	Observed
Run I.	712	530	712	893
Run II.	712	553	712	870
Run III.	712	460	712	963
Totals	2136	1543	2136	2726

DISCUSSION AND CONCLUSIONS

This all means, as several writers have stated before, that well-shaped natural oysters do have a very strong tendency to land right side up when planted single in the water. One might say that well-shaped oysters are fitted to fall through the water in a way that is most likely to lead to survival after the oyster strikes the bottom. We might wonder what circumstances throughout the ages would cause a natural oyster to fall through the water and what would cause these helpless invertebrates to be so attuned to the environment in this respect. But whatever the situation, they are obviously among the most successful marine animals on Earth being present in all continents except Antarctica, at depths from the surface to

two kilometers, and in such abundance that they leave organic remains such as the Point au Fer Reef in Atchafalaya Bay in Louisiana which was 30 miles long in its heyday. As relicts of one single animal these are probably the largest conglomerations on Earth, for the sometimes larger coral reefs are formed from the remains of many species of animals and plants.

Observations made by the scuba divers (W. D. Burke, Ron Lukens and John DeMond) showed that oysters thrown overboard with a shovel stabilized themselves within two feet and then continued to fall in the same way to the bottom. This confirms the previous statement of Needler who implies that oysters were held in various positions at the surface and then released. Looked at another way, our results indicate that well-shaped oysters have a 36% better chance of survival on soft mud where they would die less quickly than misshapen oysters which might fall wrong 59% of the time as indicated by Gunter and McGraw (1974).

Examination of Table 1 shows that oysters falling through the water in the proper stance, so to speak, have a tendency to do so on repeated trials, whereas oysters that fall upside down have a similar tendency to continue to fall upside down

with repeated trials. This is the conclusion we would expect if the shape of the oysters modifies its manner of falling through the water.

The matter of how well oysters survive on various bottoms when they fall upside down or right side up is another question and although at first blush it might seem to be simple, easy and clearcut, it is a bit more complicated than it first appears. Be that as it may, we hope to treat that subject in a subsequent study.

ACKNOWLEDGEMENTS

We thank Mr. Ronald Lukens and Mr. John DeMond for assisting us with the diving and Mrs. C. E. Rasor and Mr. Anthony Becker for the use of their swimming pools.

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AN ANALYSIS OF OYSTER HATCHERY PRODUCTION OF CULTCHED AND CULTCHLESS OYSTERS UTILIZING LINEAR PROGRAMMING TECHNIQUES

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ABSTRACT

Manpower and operational requirements for cultched and cultchless oyster production schedules in a large-scale hatchery were compared using a system of linear equations and a computer optimization program. The matrix of equations defined the operational sequence within the oyster hatchery, the resource requirements, and restrictions, if any. The optimization program minimized a cost objective function within the constraints defined by the system matrix.

Data for the calculations of the matrix coefficients were taken from records of the University of Maryland small-scale hatchery and from Dupuy (1973). The hatchery data provided estimates of manpower requirements for each activity, oyster mortality rates, and equipment costs. Dupuy's paper provided space and density requirements. The temporal sequence of oyster development stages was based on well-documented literature and observations at the model hatchery.

Results show that labor was the major cost component in all types of hatchery schedules. The optimal solution involved purchase of large amounts of equipment which remained idle most of the year, being fully utilized in two pulses during the year. Constant maximal use of equipment required less equipment but more labor and therefore increased production costs. Use of the cultched mode of hatchery operation as opposed to the cultchless resulted in approximately 45% savings in production costs.

This study represents the first phase of a long-term project to optimize production scale oyster hatchery operations. Several problem areas indicated by this model will be investigated and changes incorporated into a revised formulation.

INTRODUCTION

This paper describes a mathematical model of the operation of a commercial oyster hatchery. Through linear programming (LP) techniques the model has been used to: (1) determine an optimal production schedule and equipment mix for oyster hatcheries, (2) compare hatchery production of

cultched spat to cultchless spat; and (3) test the design of a production scale oyster hatchery just completed at the UMCEES Horn Point Environmental Laboratories Cambridge, Maryland. The goal of this paper is to demonstrate the utility of LP as a tool for economic analyses in production aquaculture.

Linear programming is a mathematical technique which determines optimal levels of activity

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within given resource restrictions, using well-documented theory (Gass, 1969) and readily available computer programs. As an analytical tool, linear programming has been used in a variety of biological applications (Arroyo, 1965; Davis, 1967; Swartzman, 1973.) The model form is a matrix of linear equations describing the production or use of restricted resources. The use of linear equations assumes all functions modelled to be linear, thereby precluding economies of scale and exponential cost curves. Since matrices of this form generally have a large number of possible solutions, an additional equation, the objective function, can be defined which is maximized within the given set of possible solutions to the matrix. For example, an objective function could be a series of terms relating the profit in all of the activity levels, thereby determining the most profitable solution consistent with the imposed constraints.

METHODOLOGY

The temporal sequence used in the model consisted of a 360-day year divided into a 300-day production period, a 30-day maintenance period, and 30 days of vacation. The oyster life-cycle was divided into 15-day periods to consolidate the model activity into units closely approximating life stages of oysters in the hatchery culture procedure. The life-cycle activities and their durations (Table 1) for cultchless hatchery operation are based on observations at the University of Maryland Horn Point hatchery. Each of the life-cycle activities could be initiated in any of 20

TABLE 1. *Definitions and Durations of Life-cycle Activities Available for Initiation during the Production Year.*

No.	Activity	Duration (Periods)
1	Grow 1 carboy of algae	1
2	Condition 1 oyster	3
3	Fill 1 Larval Cone (600,000 larvae/cone)	1
4	Set and harden 1 Mylar sheet of oysters	2
5	Fill 1 trough with oysters for final hardening	4
6	Heat water to condition oyster for 1 period	1

periods, although the developmental biology in the oyster life-cycle obviously precluded certain choices such as initiating spat set prior to the conditioning and larval stages.

Listed in Table 2 is a set of activities through which the model could purchase resources, such as labor and equipment, necessary to conduct the hatchery operations. Initiation of these activities (i.e. purchasing of resources) took place prior to the production year and permitted use of the purchased items throughout the year. This restriction precluded purchase of additional equipment or temporary labor during the production year. Labor to install purchased items is included in the cost.

TABLE 2. *Purchasing Activities and Associated Costs Initiated Prior to the Production Year.*

Activity	Cost U.S. Dollars
Hire labor to work 8 hrs/day for 15 days	10,000
Buy 1 carboy	15
Buy 1 Larval cone	250
Buy 1 spat tank and set of associated Mylar trays	1,180
Buy 1 sq. ft. of hardening trough	5
Buy 1 conditioning tank (9 sq. ft.)	100

The resource equations for a period in mid-year are shown in Table 3. The matrix coefficients are the levels of the resource (manpower, equipment or energy) required per unit of hatchery activity. For example, growing a carboy of algae (activity 1) would require 1 carboy, 30 hours of labor and produce 55.8 liters of algae with a mean cell concentration of 10^7 cells/ml. The negative sign indicates production as is illustrated in the following equation:

$$-55.8X_1 + 84X_2 + 240X_3 + 75X_4 \leq 0$$

Addition of 55.8 to both sides produces an equation which limits utilization of algal food to less than or equal to the algal production. Production in successive periods is linked by use of this convention. Thus, larvae initiated in period 5 and grown for 15 days would add to the supply of spat for use in the period 6 activity of hardening the spat on Mylar sheets.

TABLE 3. Matrix Coefficients for Cultchless Hatchery Production Activity Initiated During a Mid-Year Period.

Resource	Activity					
	X ₁	X ₂	X ₃	X ₄	X ₅	X ₆
No. of carboys	1					
Sq. ft. conditioning space		.25				
No. of larval cones			1			
No. of spat tanks				1		
Sq. ft. of trough					1	
Labor (hours)	30		65.25	39	.625	
Liters of food supply (Algal)	-55.8	84	240	75		
Larval supply (Individuals)		-60,000	600,000			
1st hardening spat supply (Individuals)			-240,000	120,000		
Final hardening spat supply (Individuals)				-60,000	1	
Hot water (gpm)		.004				-30
Oysters (Individuals)					-1	

X₁ = Grow 1 carboy of algae
 X₂ = Condition 1 oyster
 X₃ = Grow larvae
 X₄ = 1st hardening
 X₅ = Final hardening
 X₆ = Heat water

The coefficients in Table 3 were calculated from the records of a small scale oyster hatchery that was operated for one year at Horn Point Environmental Laboratories. Labor coefficients were developed on the assumptions of U.S. union labor (i.e. 40 hr work week and 30 day annual leave). The design of a cultchless hatchery and its requisite space, oyster density requirements, and flow rates for water were taken from Dupuy (1973). The costs for purchase of equipment supplies and expendible materials are actual figures for (1976) construction of a pilot production hatchery currently in operation at Horn Point.

A cost objective function was chosen for this model utilizing the costs for purchasing the resources listed in Table 2. The life-cycle activities also had associated costs, though they were small compared to the costs of materials, labor, and energy.

RESULTS

The initial computer run of the model was made to optimize the production schedule and minimize the amount of labor, space, and equipment required to produce 50 million oysters in the 10-month cultchless production period. The resource

requirements and production schedule to meet this constraint are shown in Figure 1. Since the initial high level of conditioning activity (labelled A), propagates through subsequent life stages, fully utilizing the purchased resources, new conditioning activity (labelled B,C,D) during the first 10 periods is either low or non-existent. After the pulse of activity passes out of the system, (e.g. oyster spat are planted on natural bottom), a new high level of activity (labelled E) is initiated.

A typical pattern of equipment utilization shows an initial maximal use followed by several periods where the equipment is largely idle. This seemingly non-optimal solution on closer examination was found to be soundly based. Since labor to use the equipment was by far the greatest cost element in the objective function, the model utilized a mobile labor force shifting from equipment types as it followed the oyster life-cycle.

It is possible within the LP framework to restrict the level of an activity within a given range, thereby obtaining a solution in which the hatchery equipment was more fully utilized in all periods. The oyster conditioning was therefore constrained to a level of activity currently used in the HPEL pilot production hatchery. This restriction limited

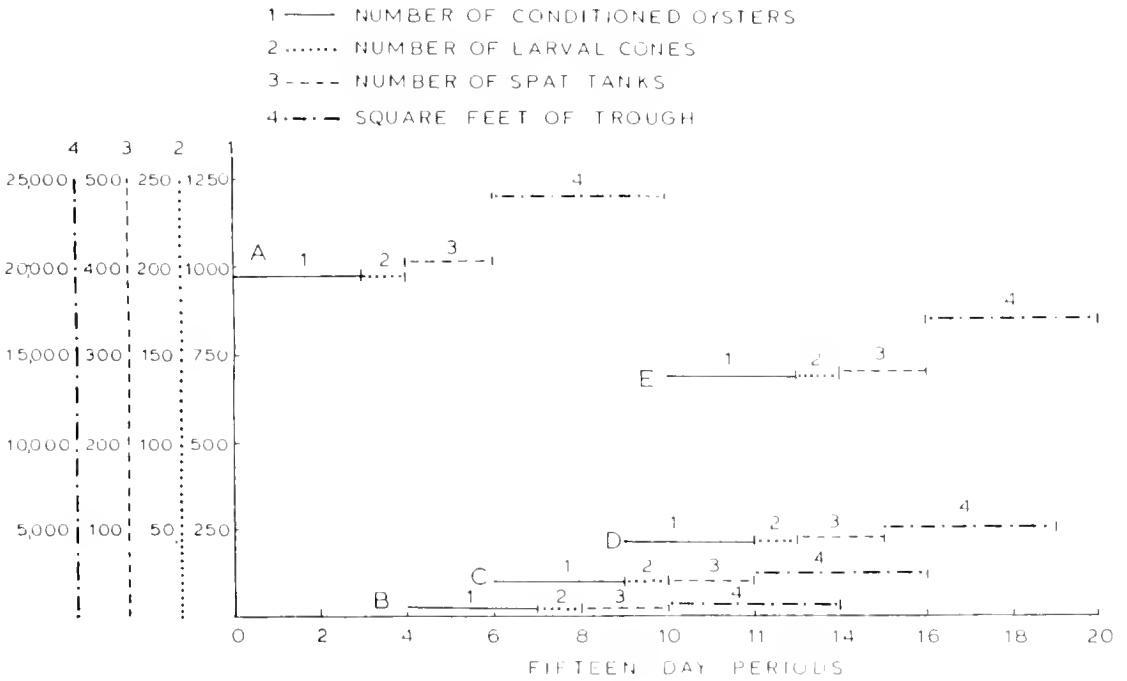


FIGURE 1. Time sequence and activity levels for 50 million oysters/year.

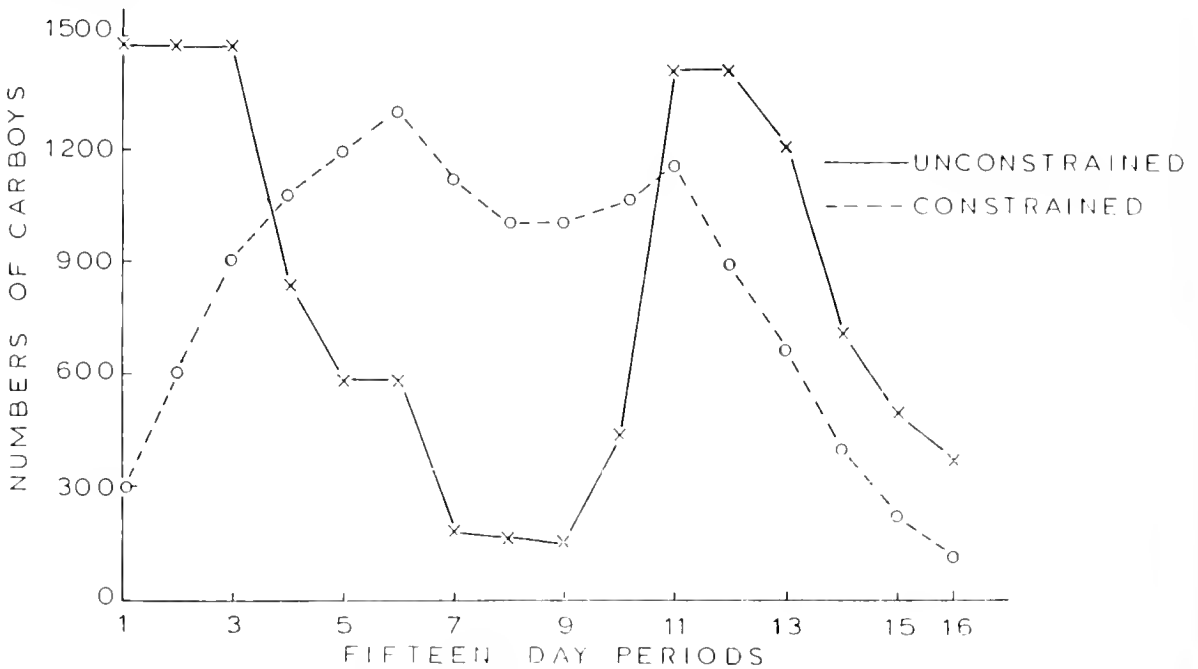


FIGURE 2. Carboy utilization for algal culture.

all subsequent life stages and activities. Figure 2 compares the time sequence of a particular resource for the constrained and unconstrained modes of operation. The number of carboys utiliz-

ed is less for the constrained mode and the number of periods in full use is longer than the unconstrained mode. Table 4 lists all of the equipment and labor needs for these two possible hat-

TABLE 4. *Resource Requirements for Constrained and Unconstrained Brood Stock in a Theoretical Hatchery Design to Produce 50 Million Oysters Per Year by the Cultchless Hatchery Process.*

Resource	Not Constrained	Constrained Brood Stock
Cost (\$1000)	2,688	2,968
Carboys (#)	1,469	1,531
Condition (sq. ft.)	27	23
Cones (#)	195	80
Spat Tanks (#)	407	191
Troughs (#)	1,017	995
Manpower	291	376

chery production schedules. The constrained solution costs more because of the increased labor costs associated with conducting several operations simultaneously as opposed to shifting the labor force from activity to activity as the production pulse passes through the system.

The cultched mode of hatchery operation was modeled by removing the first hardening activity (X₁) and putting all newly set spat directly into the hardening troughs. The number of periods required for maturation was increased to 90 days (6 periods). Table 5 compares the results of this run with the requirements for production of 50 million oysters by the cultchless production method. The total cost for production of spat on cultch was 44% less than by the cultchless method partially because of space economies and greater survival after setting, but mostly as a result of the lower labor requirements.

Finally, the cultched and cultchless modes were compared using the actual equipment and space available for the operation of a full scale production hatchery at Horn Point. An unrealistic assumption allowed the hatchery program to hire unlimited labor, though the cost of the labor to conduct the various specific procedures remained constant. An oyster selling activity (\$100/1000 oysters) (10c each) was added to replace the pro-

duction quota as a motivating force for the model. The results in Table 6 indicate a non-optimal purchase of equipment when the hatchery was designed. The non-starred equipment remained idle, limited by the starred resource. The model output permits calculation of the percent of idle equip-

TABLE 5. *Resource Requirements for Comparison of Cultchless and Cultched Hatchery Procedures. Production of 50 Million Oysters Per Year.*

Resource	Cultchless	Cultched
Cost (\$1000)	2,688	1,503
Carboys (#)	1,469	753
Condition (sq. ft.)	27	14
Cones (#)	195	100
Spat Tanks (#)	407	—
Troughs (#)	1,017	1,042
Manpower	291	195

TABLE 6. *Comparison of Resources in HPEL Hatchery Under Cultched and Cultchless Operation Using a Profit Objective Function.*

Resource	HPEL Hatchery Design	
	Cultchless	Cultched
Profit (\$1000)	175.4	366.9
Carboys (#)	103	101
Condition (sq. ft.)	15	17
Cones (#)	6	13
Spat Tanks (#)	12*	—
Troughs (#)	60	140*
Manpower	37	45
Oysters (X1000)	4,320	6,720

*Limiting Constraints

ment thereby providing guidance for the optimal hatchery design. Within the given resource restrictions the cultched mode again was more efficient than the clutchless mode producing more oysters (48%) than the cultchless mode.

CRITIQUE OF THE MODEL

This model represents the first phase of a long term project to determine the economic and biological feasibility of using hatchery-raised oysters to sustain public and private oyster fisheries. The modeling effort, in conjunction with existing conventional biological research programs, has demonstrated some uses as a tool in determining the future of aquaculture in the Maryland portion of Chesapeake Bay. These uses include satisfying the initial objectives of optimizing a production schedule and equipment mix for oyster hatchery production, pointing out contrasts between cultched and cultchless hatchery operation and identifying potential production bottlenecks due to design errors. Beyond these important products, modeling efforts can benefit research by clearly and formally organizing data on hatchery operation, and indicating where carefully planned new research or technical improvements could be of greatest benefit.

Analysis of the output from this initial modeling effort suggests several areas which need more refined equations and/or more data from the actual operation of a production scale shellfish hatchery which produces both cultched and cultchless oyster spat. Operational manpower and production calculations were based on figures from a laboratory scale hatchery which set only 10 million spat in 1976. A great economy of scale which the linear program framework cannot model, is expected in the operation of a larger facility in 1977 which should produce 100 million spat during its first year of operation. Therefore,

during 1977, the HPEL facility is being devoted to collection of the types of data necessary for the reformulation of the model. The reformulated model in addition to performing tasks illustrated in this report can then be used as a predictive tool, allowing production modifications to be tested without disrupting hatchery operation.

ACKNOWLEDGEMENTS

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GREGARIOUS SETTING IN EUROPEAN AND
AMERICAN OYSTERS — RESPONSE TO
SURFACE CHEMISTRY vs. WATERBORNE PHEROMONES¹

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ABSTRACT

Action of a waterborne pheromone in gregarious setting was demonstrated by exposing European oyster larvae to extrapallial fluid (EPF) prior to and during exposure to cultch shell. Both treatments resulted in significant increase in larval setting over controls, indicating that the setting response can be released without contact with a treated cultch surface. Cross reactivity of EPF between American and European oysters was also indicated. Additional experiments should investigate the role of the pheromone in planktonic movements of larvae.

INTRODUCTION

In 1949, Cole and Knight-Jones discovered "gregarious setting" in the European oyster, *Ostrea edulis* L. larvae. The presence of postmetamorphic oysters stimulated, in some manner, the setting of larvae near the site. The authors surmised that a waterborne material released by the juveniles stimulated the mature larvae to set. Since that time British workers have held the strong opinion that gregarious setting is mediated by the direct contact of larvae with compounds adhered to the setting surface (Crisp,

1965, 1974; Bayne, 1969). Various test materials, i.e., fractionated oyster tissue extracts and extrapallial fluid (oyster shell liquor), they state, were effective only when applied to surfaces. When test chemicals were administered in suspension or solution there was no observable modification of the behavior of the larvae and a change in setting rates did not result. They speculate that it would be improbable that a larva could respond to a waterborne material because of very low concentrations of the material in all but the immediate source area (boundary layer theory). Further, they hypothesize that a small animal, such as an oyster larva, could not sense a concentration gradient

¹ Ira C. Darling Center Contribution No. 119

and that their swimming speeds are so low that they could not effectively approach the source (Crisp, 1965).

Our developing information with the American oyster (*Crassostrea virginica*), however, indicates the action of a waterborne pheromone (Hidu, 1969; Keck et al., 1970; Veitch and Hidu, 1971). Spat enclosed in bags of plankton mesh too small for passage of larvae stimulated setting on cultch outside the bags. Addition of extrapallial fluid (EPF) or seawater which had contained adult oysters significantly increased setting rates within one to two hours. Of course, there is the possibility that the administered materials became adhered to the cultch surfaces and the larvae responded to surface contact after all, as suggested by Crisp (1974).

To really understand and manipulate recruitment in oysters it is important that we determine the mechanisms of action in gregarious setting, i.e., response to surface attached molecules and/or response to waterborne materials. A setting response released only after surface contact would mean that mature larvae are benthic and undergo extensive random "searching" of the bottom until the "proper" substrate is encountered. With the relatively low current velocities just at the bottom and feeble swimming speeds of larvae, it is difficult to conceive how a surface contact response alone could be of significant benefit in increasing the efficiency of setting of larvae. Rather, the response would be highly adaptive if pelagic mature larvae could sense the presence of a large adult population and then become benthic and set in the immediate area. Indeed Welch (1930) and Crisp (1965) suggested such a mechanism; the response to a dissolved chemical being coupled to a second sense, i.e., a light response. Photopositive larvae would turn photonegative, thus causing the larvae to reach a desirable setting area. This behavior, possibly coupled with the response to specific surface chemistry, would be more advantageous to the setting larvae. Thorson (1964) suggested that oyster larvae were photopositive throughout their larval life, but then turned photonegative and set in response to environmental stimuli such as increased temperatures encountered in the intertidal zone. The sudden appearance of the larval eyespot just prior to setting

is highly suggestive that this receptor is functional in setting in some manner.

In the present experiments, European oyster larvae were exposed to extrapallial fluid applied in suspension prior to and during exposure to cultch shells in order to demonstrate the release of a setting response through the waterborne action of the setting pheromone. Further, the cross reactivity of EPF of American and European oysters has been determined for these species.

This study was supported in part by National Science Foundation Grant No. GA-28741 and by NOAA, Office of Sea Grant, Project No. NG-40-72.

MATERIALS AND METHODS

All tests determining effects of EPF on setting were conducted in a similar manner. European and American oyster larvae were first reared by methods described by Walne (1966) and Loosanoff and Davis (1963).

Trials were run with eyed larvae which had initiated setting in large 400-liter culture vessels. Larvae were concentrated from the larger vessels and then aliquoted into a series of 1-liter beakers which each contained five bay scallop, *Aequipecten irradians*, shells as cultch. Each beaker contained approximately 5000 larvae with five to ten replicates per treatment. Twenty-five mls of EPF was added to 1-liter of larval suspension in the appropriate series. The experiment was then held for one to two hours to allow significant numbers of larvae to attach to the shell cultch. All vessels were then emptied at the same time and the cultch shells were gently dipped in clear seawater to remove larvae from the shells that had not set. This process, no doubt, removed some newly set larvae; however, all repetitions were carried out in a uniform fashion to permit a valid measurement of the effect of the treatment on setting. Cultch shells were dried and the total number of larvae that set were counted under a binocular microscope. The results were analyzed by calculating the 95% confidence limits of the mean, $\pm 2 SE_m$, or by subjecting results to a single classification ANOVA where appropriate (Steel and Torrie, 1960).

Extrapallial fluid, intra- and interspecies trials. The effects on setting of EPF administered in suspen-

sion, was determined first at the intraspecies level and then at the interspecies level. With American oysters, an initial series of 12 experiments tested the effects of American oyster EPF by comparing setting rates with untreated controls. Later, a single experiment determined the effects of European oyster EPF on American oyster setting by comparing its performance with American oyster EPF and untreated controls. Similarly, with European oysters, 7 experiments were performed to determine the effects of intraspecies EPF and two with interspecies EPF. Significant differences in oyster set between control and EPF treated cultures within each experiment were determined by a "t" test (Steel and Torrie, 1960).

American oyster EPF was procured by first holding in-season scrubbed oysters out of water for two to three hours. The shells were then gently pried open with an oyster knife and the EPF removed. This procedure generally produced several mls. of a rather viscous yellow fluid with a protein concentration of 90 to 100 ug/ml. This procedure was not possible with European oysters because this species retains less EPF and prying of the fragile shells resulted in damage to our valuable brood stock animals. An alternate method was devised, that of allowing 36 air-dried oysters to pump in a single 3-liter volume of sea water for two hours. Oysters readily transferred EPF to this medium; however, the protein concentrations were much lower, approximating 20 ug/ml.

Extrapallial fluid — action of waterborne vs. attached chemicals.

We felt that waterborne action could be further demonstrated if prior exposure of oyster larvae to EPF in suspension resulted in increased setting rates after transfer to experimental cultures containing only seawater and cultch, but no EPF. A series of four experiments was thus set up to determine setting rates for European oyster larvae which were pretreated in two ways (Figure 4). The first group was held in a 60-liter vessel with the addition of 6 liters of EPF from European oysters (procured as above). Larvae were stirred to prevent prolonged contact with container surfaces. After 10 minutes, larvae were decanted onto a sieve, thoroughly washed with filtered seawater and placed in a second 60-liter vessel made up to

the same volume with EPF-free seawater. A second 60-liter vessel with larvae served as a control. Concentrations of larvae in the vessels approximated 5000 per liter.

Three experimental treatments were initiated, i.e.,

- a. Control larvae with no EPF (10 reps)
- b. Control larvae with 25 mls EPF added to experimental cultures
- c. Experimental larvae pretreated with EPF but with no addition of EPF to experimental cultures. (EPF released).

Results from each of the four repetitive experiments were analyzed with a single classification ANOVA. Significant differences among treatments were determined with an lsd test (Steel and Torrie, 1960).

RESULTS

Intraspecies response to EPF. Extensive trials with American and European oysters indicate that there is a very rapid response to EPF administered in suspension (Figure 1). One to two hours of ex-

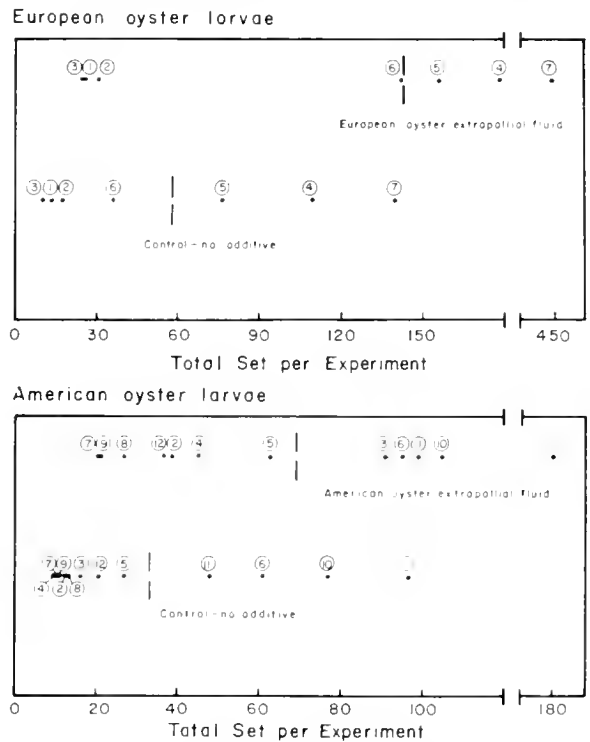


FIGURE 1. Setting of European and American oyster larvae in response to intraspecies extrapal-

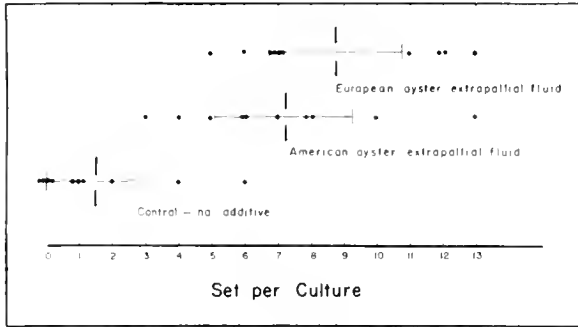
lial fluid administered in suspension. Seven experiments were run with European oyster larvae and 12 with American oysters, with ten replicate cultures in each experiment. "T" tests revealed significant differences in all experiments at least at the 95% level.

posure resulted in over twice the setting in experimental cultures. Gross examination revealed that setting behavior is activated within 10 minutes of application of EPF. Shells extracted from experimental cultures at this time had greater numbers of larvae loosely attached in a swim-crawl phase preparatory to setting.

Additional trials with both species indicated a possible interspecific response, although the results were variable for unknown reasons. With

European oyster larvae, for example, a first trial with American oyster EPF (Figure 2) resulted in a very significant increase in setting rates. A second trial, however, resulted in a very little increase over untreated controls. A preliminary trial with American oyster larvae indicated increased setting in response to European oyster EPF (Figure 3).

European oyster larvae Expt. 1



European oyster larvae Expt. 2

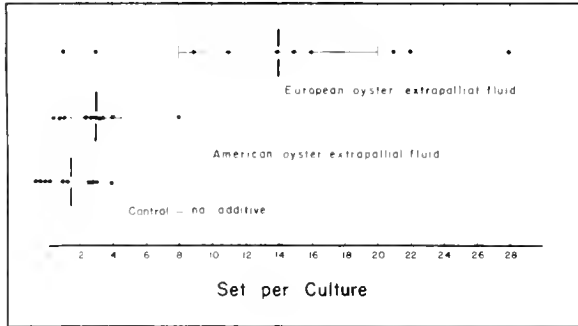


FIGURE 2. Setting of European oyster larvae in response to extrapallial fluid of American and European oysters. Points indicate replicate cultures within each experiment. Mean values of replicates and 95% confidence limits ($\pm 2 SE_m$) are indicated.

American oyster larvae

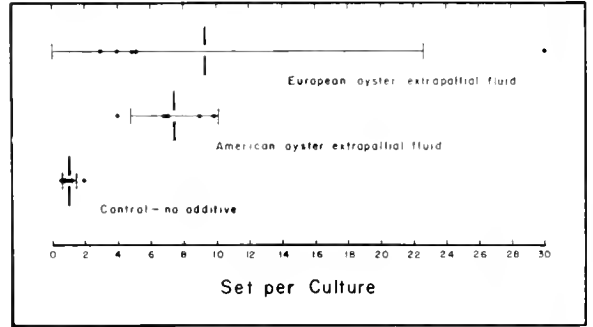


FIGURE 3. Setting of American oyster larvae in response to extrapallial fluid of American and European oysters. Points indicate replicate cultures with mean value and 95% confidence limits indicated.

Exposure of European oyster larvae to EPF prior to exposure to cultch shells resulted in significant increases in setting, demonstrating a waterborne action of the pheromone (Figure 4). Two of four repetitions of the experiment resulted in significant differences between treatments, with controls being significantly lower than the groups exposed to EPF and rinsed, which were in turn lower than the groups exposed to EPF during the exposure to cultch shell. Two other experiments, although they showed similar numerical trends showed no overall significant differences as revealed by the ANOVA.

Thus, oysters of both species are immediately stimulated to set in response to EPF administered in suspension. The response appears to be interspecific. The action of a waterborne material is indicated with European oysters because the larval setting response was released by exposure to suspended EPF prior to exposure to cultch shells.

EUROPEAN OYSTER SET				
Expt.	Control	EPF Released		EPF
1	51 (Total of 10 cultures)	< 83	<	121 **
2	100	= 141	=	130 NS
3	60	= 99	=	124 NS
4	7	< 114	<	414 **
Total	218	437		789

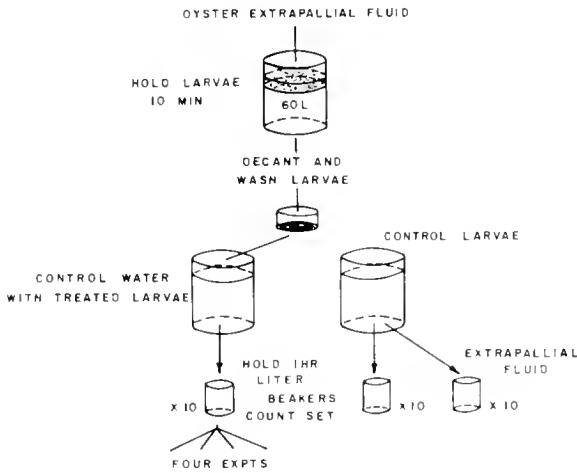


FIGURE 4. Setting of European oyster larvae in response to intraspecies extrapallial fluid administered prior to and during exposure to cultch shells. An appropriate ANOVA analyzed significance of differences in each of four experiments.

DISCUSSION

These experiments add evidence that oyster setting is initiated through action of waterborne chemicals. Thus there appears to be an additional component to the gregarious setting response not generally recognized by the British workers. However, the mechanism of action of waterborne materials is obscure, again by reasons stated previously. The attractive option is that waterborne pheromones present in the vicinity of very large concentrations of oysters act to draw larvae from the plankton by modifying their photo- or geotaxis. American oyster populations, in the American mid-Atlantic region at least, in their undisturbed state are, or were, concentrated on huge bars of many acres surrounded by vast expanses

of mud bottom. It would be quite expedient for larvae to "recognize" these areas, drop from the plankton, and begin exploring the bottom, with then at least some chance of encountering a favorable attachment surface.

We have tried to measure change in larval geo- and phototaxis by administering EPF under conditions of light and dark in small-scale water columns. Results were interesting but inconclusive because of inadequate experimental apparatus. Needless to say, it would be very instructive to demonstrate positive geotaxis or negative phototaxis which is released by the presence of waterborne chemicals from oysters. Realistic-sized experimental water columns with precise control of environmental factors would be a necessity.

These experiments indicated considerable cross reactivity of EPF between *Crassostrea* and *Ostrea*, and this suggests that chemicals emitted from oyster populations may modify recruitment rates in other species; that is, act as kairomones as described by Kittredge et al (1974). It is not hard to imagine the adaptive value of such evolution; predators may locate prey (Welch, 1930; Crisp, 1965); larvae of epifaunal species may detect a substrate favorable for epifauna; finally the most intriguing possibility, interspecies setting responses may be the biological basis for the establishment of many marine benthic communities. The British (Meadows and Campbell, 1972) appear to have considerable evidence for interspecies response for many groups but tend to dismiss its importance in favor of the dominant intraspecies response. Much remains to be accomplished in determining the ecological significance of the chemical senses in marine meroplankton, but their potential diversity of form and function cannot be disputed at this point.

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SOME OBSERVATIONS ON THE OCCURRENCE OF
PEARLS IN THE BLUE MUSSEL,
MYTILUS EDULIS L.¹

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ABSTRACT

*Pearl incidence in raft and shore populations of mussels (*Mytilus edulis* L.) of similar lengths was quantitatively compared in four separate experiments in the Damariscotta River and Boothbay Harbor, Maine. Highly significant differences between the two population types were found in each of the experiments, with fewer and smaller pearls occurring in raft-based individuals. A positive correlation was observed between the number of pearls in mussels of similar lengths sampled from each of the rafted populations and the amount of time the rafted substrate had been in the water. The relationship between number of pearls per mussel and age was quantified for one rafted and one shore population of mussels in South Bristol, Maine. No significant age-independent differences were found between the two populations with regard to the quantity of pearls present. Quantification of differences in pearl incidence between geographically isolated *Mytilus edulis* populations should facilitate correlation of the presence and quantity of pearls with the presence and abundance of the definitive and/or intermediate host(s) of the digenetic trematode parasite reputedly responsible for the initiation of pearl formation.*

INTRODUCTION

According to Giard (1907), the first documented account of the presence of pearls in mussels (*Mytilus edulis* L.) was given by Olaus Worm in 1655 upon examination of mussels taken near Copenhagen. Since that time, various workers have commented on the presence of pearls in isolated *M. edulis* populations. European investigators have reported pearl-infested mussels in a number of localities along the coasts of Denmark, France, and England (Garner, 1857; d'Hamonville, 1894; Dubois, 1901, 1909; Jameson, 1902; Herdman, 1904; Giard, 1907). Stafford (1912)

isolated pearls from specimens of *M. edulis* sampled from certain areas along the Gaspé coast of Canada. More recently, Scattergood and Taylor (1949) have reported pearls in various mussel populations along the northeast coast of the United States from Eastport, Maine, to Cape Cod, Massachusetts. In all of the studies above, considerable variation in both number and size of pearls with geographical location has been reported. Such variable incidence has resulted in the designation of distinct pearl-producing areas and is of considerable biological interest. Factors responsible for the observed differences have been the research subject of several workers (Garner, 1872; Dubois, 1901, 1909; Jameson, 1902; Scattergood and Taylor, 1949).

The independent studies of Garner (1872) and

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Dubois (1901) showed pearl incidence in *M. edulis* to result from infection by a parasitic trematode. Jameson (1902) described the organism which, according to Odhner (1905), is probably *Gymnophallus bursicola*. Since Jameson's description, considerable work has been done to ascertain the life cycle of the distome parasite (Odhner, 1905; Nicoll, 1906; Giard, 1907; Dubois, 1907a, b, 1909). Thus far, the suggested life cycle involves either the common eider duck, *Somateria mollissima*, and/or the black scoter, *Oidemia nigra*, as the definitive host(s) and the blue mussel, *M. edulis*, as the intermediate host (Dubois, 1907b; Jameson and Nicoll, 1913; Stunkard and Uzmann, 1958). Whether a second intermediate host is required remains uncertain (Nicoll, 1906; Dubois, 1909; Stunkard and Uzmann, 1958). In general, therefore, the life cycle of the trematode is not well established and attempts at further unravelling the cycle have been frustrated largely because of taxonomic chaos. This is emphasized by the statement of Stunkard and Uzmann (1958, p. 298), "specific identification (of gymnophallids) is so uncertain that we prefer to list the worms by host and location rather than propose names that might further confuse the taxonomic situation."

During the past century, various workers have speculated on factors responsible for the presence or absence of pearls in various populations of mussels (and, hence, factors controlling the distribution patterns of the trematode initiating pearl formation). Of these, salinity has been alluded to by two workers. Jameson (1902, p. 143) stated that the "most favorable places (for pearl formation) seem to be estuaries or landlocked channels", while Dubois (1909) observed that pearl-bearing populations were frequently located at the mouths of rivers. d'Hamonville (1894), studying a bed of "*moulières perlières*" in Billiers (a borough in Brittany, France near the mouth of the Vilaine), could detect no differences between various environmental parameters (sediment, current velocity, seaweed distribution, and plankton) of the pearl-infested area and those of an adjacent area harboring "*moulières sans perles*". Lack of contact of the mussel with the sediment has been suggested as contributing to reduced pearl incidence by both Jameson (1902) and Nicoll (1906) based on studies of the creeping motion of the sup-

posed cercaria of the gymnophallid responsible for initiation of pearl formation. Furthermore, Jameson (1902) observed reduced pearl incidence in mussels taken from stakes or floating objects, although Dubois (1909) found pearls within *Mytilus galloprovincialis* on ropes in the experimental culture operations at the University of Lyon. A final factor, and one which has received only limited attention, is that of age. d'Hamonville (1894) commented that pearls were only found in the largest and less regularly formed mussels ("*celles qui sont le moins régulièrement formées*") at Billiers, while Jameson (1902) observed that pearls were seldom found in mussels less than 40 mm in length. These stunted and larger individuals may well have been the older members of the population. Jameson (1902) attributed the relatively small size of pearls in the Billiers population to the active mussel fishery in the area which prevented individual mussels from reaching "a great age". The effect of age is summarized by Jameson's (1902, p. 162) statement that the "general experience of everybody acquainted with pearl-fisheries is that the largest pearls were found in the oldest and thickest shells, which proves how intimately the growth of pearl and shell are associated." Despite this realization, no workers have attempted to quantify the relationship between the presence of pearls and age. Furthermore, it has never been demonstrated that age-independent differences exist between various populations with regard to the size and quantities of pearls present. The lack of such quantitative data in these studies renders conclusions concerning factors responsible for the presence or absence of pearls highly speculative. It is the purpose of this study to compare quantitatively the size and number of pearls in rafted and shore-based *M. edulis* populations and to establish if age-independent differences actually exist between these two population types.

MATERIALS AND METHODS

Preliminary Studies

1. Pearl Removal and Sorting

Throughout the following studies, pearls were removed from individual mussels using the following modification of the potassium hydroxide technique employed by Scattergood and

Taylor (1949). The soft tissues of each mussel were carefully removed from the shell and placed in a 5% solution of boiling KOH for a period of 10 min. This resulted in complete maceration of the tissues. The solution was diluted with water and carefully decanted, leaving the pearl-containing residue at the bottom. The residue was then poured through a specially constructed set of sieves which was rotated and gently shaken under running water for a period of 3 min. This resulted in the separation of pearls into one of the following six size categories (in microns):

(A)	> 1050	(D)	308-471
(B)	602-1050	(E)	153-308
(C)	471-602	(F)	102-153

The total number of pearls per size category was determined by examination of individual sieves under a dissecting scope. The selection of the smallest mesh (102 μm) was based on two considerations. First, the smallest diameter recorded for 486 pearls from 10 mussels was 120 μm . Secondly, no pearls were found on a 50 μm screen attached to the bottom of the sieve set during analyses of 165 mussels which contained a total of 1574 pearls.

2. Homogeneity of Shore Population

A preliminary study was undertaken in Clark Cove on the Damariscotta River in Lincoln County, Maine, to determine the variability in the number of pearls per mussel and to test the homogeneity of a shore population with regard to pearl incidence. Five stations with dimensions of 1 m² were established at the mean low water level (MLW) over a distance of 100 m, with 25 m between stations. Eleven mussels were gathered from each station, sampling only those with lengths between 63.5 and 76.2 mm (2½ - 3"). These were considered representative of the size mussels normally gathered commercially. Numbers of pearls were determined for individual mussels and the results subjected to a one-way classification ANOVA.

Shore vs Raft

Pearl incidence in raft and shore populations of mussels of similar lengths was quantitatively compared in four experiments in the Damariscotta River and Boothbay Harbor, Maine. Shell lengths of specimens sampled from the two population types in Experiments #1 - #3 were restricted to the

size range 63.5 - 76.2 mm. Lack of a sufficient quantity of rafted mussels with lengths greater than 63.5 mm in Experiment #4 necessitated the use of a smaller size range (50.1 - 63.5 mm) for adequate comparison of the two populations.

1. Experiment #1: Clark Cove Raft (3½ years)

Specimens of *M. edulis* obtained from a raft left in the water approximately 3½ years (June, 1968 - December 17, 1971) were quantitatively compared with shore specimens of similar lengths with regard to the size and number of pearls present in the soft tissues. The raft, which was located in the Damariscotta River (Clark Cove), is depicted in Figure 1. A site with dimensions corresponding to those of the raft was chosen on the shore at MLW within 50 m of the raft. The shore site and the underside of the raft were divided into five stations (Figure 1). The vertical distance between the intertidal and subtidal shore stations was less than 0.2 m. On December 7, 1971, 11 mussels were gathered from each station. The total number of pearls in each size category was determined for individual mussels and these numbers combined to arrive at station and location (shore and raft) totals. Prior to statistical analysis, a logarithmic transformation [$\log(x+1)$] (Steele and Torrie, 1960) was applied to all data since the variance was found to be approximately proportional to the square of the mean. Nested analyses of variance (mussels within stations, within locations) were run on the transformed values.

2. Experiment #2: Boothbay Harbor Raft (5 years)

Pearl incidence in mussels obtained from a raft left in the water for approximately 5 years was quantitatively compared with that in mussels of similar lengths sampled from an adjacent shore population. As in Experiment #1, a one-way hierarchical classification (mussels within stations, within locations) served as the experimental design for the following study. The raft, which had been in the water of Boothbay Harbor since July, 1967, consisted of a floating wooden bumper approximately 13 m in length. Five stations with dimensions of 1 x 0.75 m were selected on the underside of the raft. Each station was separated from the adjacent one by approximately 2 m and numbered consecutively R4A - R4E. The depth of water under the raft at mean low water varied from approximately 1 m at the inshore station

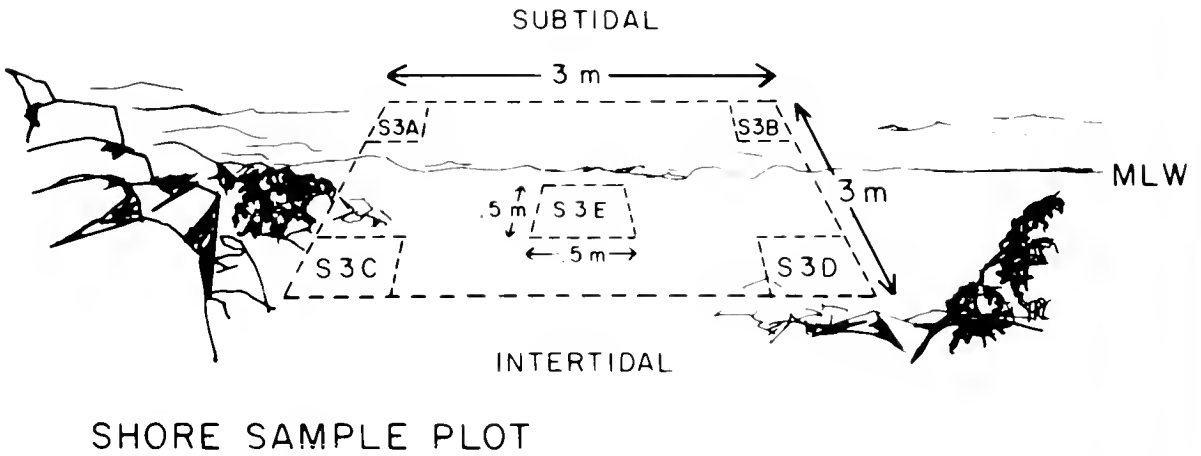
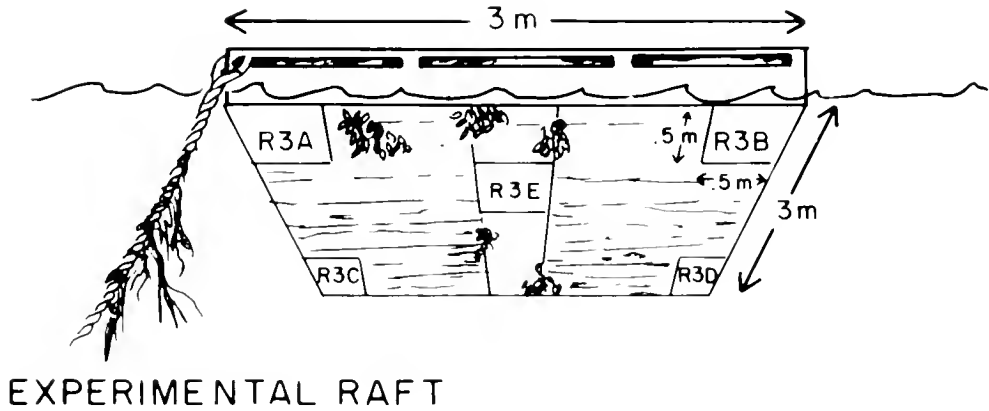


FIGURE 1. Raft and shore stations (Clark Cove, Damariscotta River, Maine) for Experiment #1. MLW - mean low water level.

(R4E) to 7 m at the offshore station (R4A). Similarly, five stations with dimensions of 1×0.75 were located on a mussel bed at MLW on the adjacent shore. Again, the stations were spaced at intervals of approximately 2 m. On August 4, 1972, 11 mussels were gathered from each of the 10 stations. The total number of pearls in each size category was determined for individual mussels and the numbers combined to arrive at station and location (shore and raft) totals. The data were transformed $[\log(x+1)]$ and the two populations compared using nested analyses of variance.

3. Experiment #3: Manila Rope (21 months)

A $5/8$ " diameter Manila rope (2 m in length) was hung from a floating dock in Clark Cove in May, 1971. On January 4, 1973, a 0.5 m section of the rope, suspended 1 m beneath the dock, was

stripped of all attached mussels. Of these, 55 specimens, varying in length from 63.5 - 76.2 mm, were sampled and subjected to the potassium hydroxide treatment. The total number of pearls in each size category was determined for the individual mussels. Through calculation of Student's *t* values, the transformed $[\log(x+1)]$ data were compared with the transformed values for the 55 mussels from the adjacent shore population described in Experiment #1.

4. Experiment #4: Asbestos Panel (7 months)

An asbestos panel measuring approximately 0.3 m^2 was placed at a depth of 1 m beneath a floating dock on the Damariscotta River (Wentworth Point) in May, 1972. On December 2, 1972, 55 mussels (from natural larval settlement) were removed from the panel and an additional 55

specimens sampled from an adjacent shore population at MLW. The total number of pearls in each size category was determined for each specimen and the transformed $[\log(x+1)]$ values for both populations compared through calculation of Student's *t* values.

Comparison of Rafted Environments

Transformed $[\log(x+1)]$ pearl counts from mussels sampled from each of the rafted environments assessed in the preceding four experiments were quantitatively compared. Seven separate analyses of variance were run comparing totals per mussel and totals for each of the six size categories. For analyses indicating a difference among a set of population means, Tukey's *w*-procedure was used to judge the significance of differences between the individual population means within the set. This test is more conservative than Duncan's multiple range test as the entire experiment is the unit used in stating the number of errors of the type where an observed difference is falsely declared to be significant. The test criterion is

$$w = q_{.05}(p, n_2)(s_{\tau})$$

where $q_{.05}$ is a tabulated value (Steele and Torrie, 1960, p. 445) for *p* treatments and n_2 degrees of freedom and s_{τ} is estimated from the error mean square. *w* is used to judge the significance at the 0.05 level of each of the observed differences (Steel and Torrie, 1960).

Shore vs Raft (Age-Independent Studies)

1. Transplantation

Pearl incidence in mussels left in a rafted environment for 14 months was quantitatively compared with that in mussels left on an adjacent shore for the same period of time. On October 19, 1972, 250 mussels with lengths varying from 13.0 - 17.0 mm were gathered from the underside of the

raft described earlier in Experiment #1. These were individually notched for subsequent identification. Twenty-five individuals were placed in each of the 10 sections (20 cm long) of cylindrical 5 mm VEXAR plastic netting with a layflat diameter of 10 cm. Five sections were hung from a raft off Wentworth Point at a depth of 0.5 m below the surface. The remaining five stations were placed in contact with sediment at the mean low water level on the shore within 50 m of the raft. On December 19, 1973, 65 of the original 125 mussels were recovered from the shore station and all 125 mussels from the raft. The pearls were removed from 65 of the 125 rafted specimens and all of the shore mussels. These were separated into size categories as previously described. Pearl counts from the two populations were quantitatively compared.

2. Regression of Pearls on Age

The regression of the number of pearls per mussel on age for a rafted *M. edulis* population was quantitatively compared with a similar regression for an adjacent shore population. On July 26, 1973, 85 mussels of 25 - 96 mm length were sampled from a raft placed in the water at South Bristol, Maine in June, 1964. Similarly, 102 mussels varying in length from approximately 19-92 mm were gathered on the same date from an adjacent shore population. The pearls were removed as described earlier and the total number per individual recorded. One shell valve of each specimen was embedded in epoxy and longitudinally sectioned along the antero-posterior axis. The exposed shell surfaces were polished and etched and acetate peels prepared for examination with both compound and dissecting microscopes. Age estimates were based on counts of annual growth patterns within the inner shell layer [See Lutz (1976) for a detailed description of annual growth patterns within the shell of both shore and raft-based specimens].¹ Occasional subjectivity associated with the counting of lines may somewhat reduce the accuracy of age estimates for certain specimens. Such subjectivity, however, is expected to be equal for both populations and should have little effect on the interpretation of differences between the two. As the variance of pearl counts for individual year classes was found positively correlated with the mean, actual counts

¹ Engle and Loosanoff (1944) found the season of setting of mussels in Milford, Connecticut, to be of comparatively short duration, extending from the early part or middle of June to the middle or end of August. Plankton samples of McAlice et al. (unpublished data) suggest that the vast majority of *M. edulis* larvae within the Damariscotta River are present between the months of May and September. It follows that the greatest proportion of larval settlement in this estuary should be restricted to these warmer months. In light of these considerations, the majority of mussels from the two sampled populations are expected to be restricted to summer year classes. Age estimates in this study are, therefore, generally considered accurate to within 1 year.

were logarithmically transformed [$\log(x + 1)$] (Steel and Torrie, 1960). A regression of transformed pearl counts on age was run for each population, using a total of 78 rafted and 82 shore specimens. Five of the original 85 rafted mussels and seven of the original 102 shore specimens were discarded because of poorly preserved peels or suspected subjectivity associated with the counting of lines. Two 1-year-old rafted and 13 shore specimens ranging in age from 10 - 16 years were also excluded because of the lack of corresponding age classes in the other population. Differences in slope and elevation between the two regression lines were assessed using an analysis of covariance (Steel and Torrie, 1960; Sokal and Rohlf, 1969).

RESULTS

Preliminary Studies

The Clark Cove shore population (at MLW) was found to be relatively homogeneous with regard to the quantity of pearls present in the soft tissues. Table 1 shows the results of the ANOVA, with the null hypothesis that no difference exists between station means other than that due to chance. The null hypothesis was accepted, suggesting that a sampling site at MLW could be located randomly at any point along the 100 m stretch with confidence of obtaining a representative sample of the population.

Shore vs Raft

Highly significant differences in pearl incidence were found between rafted and shore-based populations of mussels. In each of the four experiments, rafted individuals contained fewer and smaller pearls than mussels of similar length obtained at MLW from an adjacent shore population.

1. Experiment #1: Clark Cove Raft (3¹/₂ years)

Specimens of *M. edulis* obtained from the raft left in the water for approximately 3¹/₂ years contained significantly fewer pearls than specimens of similar length obtained from an adjacent shore population (Table 2). The nested ANOVA indicates a highly significant difference ($F = 188.83$) between the raft population mean (2.2 pearls per mussel) and that of the adjacent shore population (14.3 pearls per mussel). The null hypothesis of no significant difference between stations means was accepted.

TABLE 1. Total pearl counts and analysis of variance for mussels sampled from each of five stations at the mean low water level in Clark Cove, Damariscotta River, Maine.

Specimen	Station				
	A	B	C	D	E
1	3	14	2	2	0
2	22	2	4	12	29
3	35	8	9	0	6
4	7	61	8	10	2
5	5	18	6	3	68
6	2	11	2	1	18
7	2	0	6	2	6
8	11	9	8	16	29
9	4	10	14	4	1
10	86	6	29	9	5
11	13	6	0	13	5
Total	190	145	88	72	169
Mean	17.3	13.2	8.0	6.6	15.4
Source of Variation	df	SS	MS	F	
Among stations	4	948.90	237.20	0.84	n.s.
Within stations	50	14957.11	282.06		
Total	54	15906.01			

In addition, pearls found in the rafted mussels were significantly smaller than those obtained from the examined shore specimens. Results of the six separate analyses of variance (Table 3) illustrate that the shore population mean number of pearls in any size category is significantly greater at the 0.01 level than the mean for the raft population in any corresponding size category. Furthermore, no pearl was found in this study with a diameter greater than 1 mm in any raft-based individual. No significant differences between station means (experimental error) were shown in any of the size category analyses.

2. Experiment #2: Boothbay Harbor Raft (5 years)

Pearl incidence in mussels obtained from the raft left in the water for approximately 5 years was significantly lower than that in specimens of similar length from the adjacent shore population (Table 4). The null hypothesis (for the nested ANOVA) of no significant difference between locations (shore and raft) was rejected, with the shore population mean (27.7 pearls per mussel) considerably greater than the mean of the rafted

TABLE 2. Total pearl counts and analysis of variance for raft and shore mussels in the Damariscotta River (Clark Cove).^a

Specimen	Raft ^b					Shore ^c				
	A	B	C	D	E	A	B	C	D	E
1	1	3	0	0	0	28	2	26	15	13
2	0	1	0	0	1	11	79	7	12	9
3	12	0	1	3	0	46	13	11	3	2
4	1	0	2	18	0	8	39	5	8	2
5	8	5	0	2	10	14	1	10	38	12
6	2	0	9	2	1	5	8	0	2	1
7	1	0	0	1	5	7	3	4	17	42
8	1	7	1	0	7	15	9	14	6	10
9	0	0	3	0	5	19	3	67	5	16
10	3	1	3	0	0	14	5	5	0	59
11	0	2	0	0	2	3	7	6	16	4
Total	29	19	19	26	31	170	169	155	122	170

Raft mean = 2.25

Shore mean = 14.29

Source of Variation	df	SS	MS	F
Among stations	9	11.78	1.31	
Locations	1	11.33	11.33	188.83**
Among stations within locations (experimental error)	8	0.45	0.06	0.38 n.s.
Among mussels within stations (sampling error)	100	16.33	0.16	
Total	109	28.11		

^aThe results of the analysis of variance are based on transformed $[\log(x + 1)]$ pearl counts.^bRafted specimens were obtained from a raft left in the water approximately 3½ years (June, 1968 - December 17, 1971).^cShore specimens were gathered at the mean low water level within 50 m of the raft.

**Indicates significance at the 0.01 level.

TABLE 3. Analyses of variance for individual size category pearl counts from raft^a and shore^b mussels in the Damariscotta River (Clark Cove).^c

Size category	Population	Transformed mean	F Locations	F Experimental error
>1050 μm	Raft	0		
	Shore	0.0199	28.9043**	1.1605 n.s.
602-1050 μm	Raft	0.0748		
	Shore	0.3184	25.8653**	1.1090 n.s.
471-602 μm	Raft	0.0455		
	Shore	0.2686	21.8546**	1.2108 n.s.
308-471 μm	Raft	0.1122		
	Shore	0.4439	53.9982**	0.6080 n.s.
153-308 μm	Raft	0.1680		
	Shore	0.6293	239.8483**	0.2161 n.s.

102-153 μm	Raft	0.0917		
	Shore	0.2692	13.9485**	0.9227 n.s.

^aRafted specimens were obtained from a raft left in the water approximately 3½ years (June, 1968-December 17, 1971).

^bShore specimens were gathered at the mean low water level within 50 m of the raft.

^cThe results of the analyses of variance are based on transformed $[\log(x + 1)]$ pearl counts.

**Indicates significance at 0.01 level

TABLE 4. Total pearl counts and analysis of variance for raft^a and shore^b mussels in Boothbay Harbor, Maine^c.

Specimen	Station									
	Raft ^a					Shore ^b				
	A	B	C	D	E	A	B	C	D	E
1	1	0	2	1	0	1	75	47	16	24
2	2	0	0	97	2	12	61	4	30	0
3	4	0	0	1	0	98	5	75	5	108
4	1	12	0	0	0	1	43	15	7	9
5	2	0	144	5	0	6	18	27	13	10
6	1	0	0	1	4	25	26	35	12	8
7	1	49	12	0	4	6	13	7	4	61
8	0	0	2	0	0	4	63	7	18	1
9	0	0	1	0	0	13	20	24	7	10
10	0	0	20	1	1	64	9	5	7	27
11	3	1	1	1	0	95	57	45	75	67
Total	15	62	182	107	11	325	390	291	194	325

Raft mean = 6.85

Shore mean = 27.72

Source of Variation	df	SS	MS	F
Among stations	9	22.9170	2.5463	
Locations	1	21.3044	21.3044	105.6765**
Among stations within locations (experimental error)	8	1.6126	0.2016	0.8096 n.s.
Among mussels within stations (sampling error)	100	24.8980	0.2490	
Total	109	47.8150		

^aRafted specimens were obtained from a raft left in the water approximately 5 years (July, 1967 - August 4, 1972).

^bShore specimens were gathered at the mean low water level within 50 m of the raft.

^cThe results of the analysis of variance are based on transformed $[\log(x + 1)]$ pearl counts.

**Indicates significance at the 0.01 level.

population (6.8 pearls per mussel). The raft population, however, was extremely variable and, occasionally, individuals were found with numerous pearls (as many as 144). No significant

difference between station means (experimental error) was shown in this experiment.

In addition, the average pearl diameter encountered in rafted specimens was considerably

smaller than that encountered in shore-based individuals. As in Experiment #1, highly significant differences were found in each of the six separate analyses of variance (Table 5), indicating that the shore population mean number of pearls in any size category is significantly greater than the mean number for the raft population in any corresponding size category. No significant difference between station means (experimental error) was shown in any of the size category analyses. Only one pearl was found with a diameter greater than 1 mm.

3. Experiment #3: Manila Rope (21 months)

The total numbers of pearls in individual mussels from the rope left in Clark Cove for approximately 21 months are shown in Table 6. The calculated Student's *t* indicates a highly significant difference between the two population (rope and adjacent shore) means, with the shore population mean number of pearls (14.3) per individual considerably greater than that of the rope population (mean = 0.3 pearls per mussel).

Highly significant differences in pearl size were also found between the two populations. The actual and transformed population means, standard

deviations of the transformed means, and Student's *t* values calculated from the transformed data are summarized in Table 7 for each of the six categories. The shore population mean number of pearls in any size category was found to be significantly greater (at the 0.01 level) than the raft population mean for any corresponding size category. No pearls were found with a diameter greater than 1 mm in any of the mussels examined from the rope.

4. Experiment #4: Asbestos Panel (7 months)

Mussels obtained from the asbestos panel left off Wentworth Point for 7 months were found to be relatively pearl-free in comparison with specimens of similar length sampled from the adjacent shore population (Table 8). The actual and transformed means, standard deviations of the transformed means, and Student's *t* comparing the two population means (based on transformed data) are given in Table 8. The shore population mean (7.5 pearls per mussel) was found to be significantly greater (at the 0.01 level) than the mean of the asbestos panel population (0.1 pearl per mussel).

As in Experiment #3, highly significant dif-

TABLE 5. *Analyses of variance for individual size category pearl counts from raft^a and shore^b mussels in Boothbay Harbor.^c*

Size category	Population	Transformed mean	F Locations	F Experimental error
>1050 μm	Raft	0.0055	19.2810**	0.7291 n.s.
	Shore	0.1578		
602-1050 μm	Raft	0.0274	34.2510**	1.1684 n.s.
	Shore	0.3401		
471-602 μm	Raft	0.0930	26.8486**	0.9087 n.s.
	Shore	0.3665		
308-471 μm	Raft	0.1340	59.5426**	0.5977 n.s.
	Shore	0.5989		
153-308 μm	Raft	0.2064	44.9931**	1.4177 n.s.
	Shore	0.8966		
102-153 μm	Raft	0.1212	31.1176**	0.8762 n.s.
	Shore	0.4801		

^aRafted specimens were obtained from a raft left in the water approximately 5 years (July, 1967 - August 4, 1972).

^bShore specimens were gathered at the mean low water level within 50 m of the raft.

^cThe results of the analysis of variance are based on transformed [$\log(x + 1)$] pearl counts.

**Indicates significance at the 0.01 level.

TABLE 6. Total pearl counts from rafted mussels and results of Student's *t* test comparing these counts with counts from shore specimens.^a

Specimen	Pearls	Specimen	Pearls	Specimen	Pearls	Specimen	Pearls	Specimen	Pearls
1	0	12	0	23	1	34	0	45	1
2	0	13	4	24	0	35	0	46	0
3	0	14	0	25	0	36	0	47	0
4	1	15	0	26	0	37	0	48	0
5	2	16	0	27	0	38	0	49	1
6	0	17	0	28	2	39	0	50	0
7	0	18	0	29	0	40	0	51	0
8	0	19	2	30	0	41	0	52	0
9	1	20	0	31	0	42	0	53	0
10	0	21	0	32	1	43	0	54	0
11	0	22	0	33	0	44	1	55	0

Population	Actual mean	Transformed mean	Std. dev.	Computed <i>t</i>
Raft ^b	0.31	0.0770	0.1655	
Shore ^c	14.29	0.9824	0.4238	14.7700**

^aStudent's *t* values were calculated using transformed [$\log(x + 1)$] pearl counts.

^bRafted specimens were obtained from a 5/8" Manila rope suspended from a floating dock in the Damariscotta River (Clark Cove) for approximately 21 months (May, 1971 - January 4, 1973).

^cShore specimens were gathered at the mean low water level within 50 m of the raft.

**Indicates significance at the 0.01 level

TABLE 7. Student's *t* test results for individual size category pearl counts from raft and shore mussels in the Damariscotta River (Clark Cove).^a

Size category	Population	Actual mean	Transformed mean	Std. dev.	Computed <i>t</i>
>1050 μm	Raft ^b	0	0	0	
	Shore ^c	0.93	0.1988	0.2560	5.7620**
602-1050 μm	Raft	0.04	0.0109	0.0568	
	Shore	1.65	0.3184	0.2935	7.6303**
471-602 μm	Raft	0	0	0	
	Shore	1.45	0.2686	0.2966	6.7150**
308-471 μm	Raft	0.07	0.0164	0.0901	
	Shore	3.13	0.4438	0.3689	8.3477**
153-308 μm	Raft	0.18	0.0524	0.1218	
	Shore	5.44	0.6293	0.3868	10.5466**
102-153 μm	Raft	0.02	0.0055	0.0406	
	Shore	1.49	0.2692	0.3016	6.4317**

^aStudent's *t* values were calculated using transformed [$\log(x + 1)$] pearl counts.

^bRafted specimens were obtained from a 5/8" Manila rope suspended from a floating dock in the Damariscotta River (Clark Cove) for approximately 21 months (May, 1971 - January 4, 1973).

^cShore specimens were gathered at the mean low water level within 50 m of the raft.

**Indicates significance at the 0.01 level.

TABLE 8. Total pearl counts and analysis of variance for raft^a and shore^b mussels in the Damariscotta River (Wentworth Point).^c

Specimen	Asbestos Panel				Shore			
	Pearls	Specimen	Pearls	Specimen	Pearls	Specimen	Pearls	
1	0	28	0	1	3	28	1	
2	0	29	0	2	6	29	0	
3	0	30	0	3	3	30	85	
4	1	31	0	4	1	31	9	
5	0	32	0	5	2	32	1	
6	0	33	0	6	3	33	5	
7	0	34	1	7	10	34	5	
8	0	35	1	8	9	35	7	
9	0	36	0	9	4	36	11	
10	0	37	0	10	2	37	6	
11	0	38	0	11	1	38	12	
12	0	39	0	12	2	39	23	
13	0	40	0	13	2	40	3	
14	0	41	0	14	1	41	13	
15	0	42	0	15	3	42	4	
16	0	43	0	16	2	43	7	
17	0	44	0	17	3	44	2	
18	0	45	0	18	1	45	4	
19	1	46	0	19	1	46	0	
20	0	47	0	20	9	47	6	
21	0	48	0	21	14	48	4	
22	0	49	0	22	7	49	1	
23	0	50	1	23	2	50	4	
24	0	51	0	24	27	51	2	
25	0	52	0	25	8	52	9	
26	0	53	0	26	23	53	7	
27	0	54	0	27	10	54	16	
		55	0			55	7	
		<i>Actual</i>		<i>Transformed</i>		<i>Std.</i>	<i>Computed</i>	
<i>Population</i>		<i>mean</i>		<i>mean</i>		<i>dev.</i>	<i>t</i>	
Raft		0.09		0.027		0.087		
Shore		7.51		0.743		0.374	13.822**	

^a Rafted specimens were obtained from an asbestos panel suspended at a depth of 1 m beneath a floating dock for approximately 7 months (May - December 2, 1972).

^b Shore specimens were gathered at the mean low water level within 50 m of the raft.

^c The results of the analysis of variance are based on transformed $[\log(x + 1)]$ pearl counts.

**Indicates significance at the 0.01 level.

ferences in pearl size were also found between the two population types (rafted and shore). The actual and transformed means, standard deviations of the transformed means, and Student's *t* values

calculated from the transformed data are summarized in Table 9. The shore population mean number of pearls in any size category was found to be significantly greater (at the 0.01 level) than

the asbestos panel population mean. No pearls were found with a diameter greater than 471 μm in any of the mussels sampled from the asbestos panel.

Comparison of Rafted Environments

A positive correlation was observed between the number of pearls in mussels sampled from each of the rafted populations in Experiments #1 -

TABLE 9. Student's *t* test results for individual size category pearl counts from raft and shore specimens in the Damariscotta River (Wentworth Point).^a

Size category	Population	Actual mean	Transformed mean	Std. dev.	Computed <i>t</i>
>1050 μm	Raft ^b	0	0	0	
	Shore ^c	0.66	0.1426	0.2231	4.7375**
602-1050 μm	Raft	0	0	0	
	Shore	0.71	0.1765	0.2130	6.1498**
471-602 μm	Raft	0	0	0	
	Shore	0.64	0.1560	0.2140	5.3979**
308-471 μm	Raft	0.02	0.0055	0.0406	
	Shore	1.38	0.2746	0.2892	6.9000**
153-308 μm	Raft	0.07	0.0219	0.0789	
	Shore	3.09	0.3848	0.3648	7.3760**
102-153 μm	Raft	0	0	0	
	Shore	1.05	0.1861	0.2818	4.8974**

^aStudent's *t* values were calculated using transformed $[\log(x + 1)]$ pearl counts.

^bRafted specimens were obtained from an asbestos panel suspended at a depth of 1 m beneath a floating dock for approximately 7 months (May-December 2, 1972).

^cShore specimens were gathered at the mean low water level within 50 m of the raft.

**Indicates significance at the 0.01 level.

TABLE 10. Analyses of variance and results of Tukey's *w*-procedures for total and individual size category pearl counts.^a

Source of Variation	Total Number of Pearls			
	df	SS	MS	F
Among Rafts	3	4.7677	1.5892	15.0353**
Within Rafts	216	22.8338	0.1057	
Total	219	27.6015		
$w = q_{0.05}(4, 216)s_{\bar{x}} = 3.63(0.0438) = 0.0438$				
Raft Mean	R1 ^b	R2 ^c	R3 ^d	R4 ^e
	0.0274	0.0770	0.3402	0.3487
Size category >1050 μm				
Source of variation	df	SS	MS	F
Among Rafts	3	0.0012	0.0004	1.0000 n.s.
Within Rafts	216	0.0890	0.0004	
Total	219	0.0902		

Size category: 602-1050 μm

Source of variation	df	SS	MS	F
Among Rafts	3	0.1795	0.0598	5.5888**
Within Rafts	216	2.3123	0.0107	
Total	219	2.4918		

$$W = q_{05}(4,216)s_{\bar{x}} = 3.63(0.0140) = 0.0506$$

Raft	R1	R2	R4	R3
Mean	0	0.0109	0.0274	0.0748

Size category: 471-602 μm

Source of variation	df	SS	MS	F
Among Rafts	3	0.3259	0.1086	6.7058**
Within Rafts	216	3.4878	0.0162	
Total	219	3.8137		

$$w = q_{05}(4,216)s_{\bar{x}} + 3.63(0.0172) = 0.0623$$

Raft	R1	R2	R3	R4
Mean	0	0	0.0455	0.0930

Size category: 308-471 μm

Source of variation	df	SS	MS	F
Among Rafts	3	0.7538	0.2513	5.4869**
Within Rafts	216	9.8919	0.0458	
Total	219	10.6457		

$$w = q_{05}(4,216)s_{\bar{x}} = 3.63(0.0289) = 0.1048$$

Raft	R1	R2	R3	R4
Mean	0.0055	0.0164	0.1122	0.1400

Size category: 153-308 μm

Source of variation	df	SS	MS	F
Among Rafts	3	1.3038	0.4346	6.6069**
Within Rafts	216	14.2086	0.0658	
Total	219	15.5124		

$$w = q_{05}(4,216)s_{\bar{x}} = 3.63(0.0346) = 0.1255$$

Raft	R1	R2	R3	R4
Mean	0.0219	0.0524	0.1680	0.2064

Size category: 102-153 μm

Source of variation	df	SS	MS	F
Among Rafts	3	0.6160	0.2053	5.6093**
Within Rafts	216	7.8973	0.0366	
Total	219	8.5133		

$$w = q_{05}(4, 216) s_r = 3.63(0.0258) = 0.0936$$

Raft	R1	R2	R3	R4
Mean	0	0.0055	0.0917	0.1212

^aMussels were sampled from substrates left in the water for varying lengths of time.

^bR1 = Asbestos Panel (May, 1972 - December 2, 1972)

^cR2 = Clark Cove Rope (May, 1971 - January 4, 1973)

^dR3 = Clark Cove Raft (June, 1968 - December 17, 1971)

^eR4 = Boothbay Harbor Raft (July, 1967 - August 4, 1972)

**Indicates significance at the 0.01 level.

#4 and the amount of time for which the rafted substrate had been in the water (Table 10). The null hypothesis of no significant difference between pearl counts in mussels from the four rafted substrates was rejected for six of the seven analyses of variance (Table 10), the only non-significant difference occurring for pearls with diameters greater than 1050 μm . Although Tukey's *w*-procedure failed to show a significant difference (at the 0.05 level) between each of the individual population means, examination of the transformed means for the totals indicates a general trend for an increasing number of pearls per mussel with increasing length of submergence of the substrate from which the specimens were collected. With the exception of minor discrepancies, this same general trend holds true for the population means calculated for each individual size category.

Shore vs Raft (Age-Independent Studies)

1. Transplantation

No significant difference in pearl incidence was found between mussels left in a rafted environment for 14 months and specimens left on an adjacent shore for the same period of time. The 65 individuals which had been on the shore contained a total of two pearls. These were in two individuals and the two size categories, 102-153 and 309-471 μm . The 65 individuals examined from the raft population also contained a total of two pearls in two individuals. These were found in the two size categories, 154-308 and >1050 μm . The pearl

found in the latter size category had a diameter of approximately 1100 μm . The identical number of pearls found in each population rendered statistical analysis of the data superfluous.

2. Regression of Pearls on Age

No significant age-independent difference in the number of pearls within the soft tissues was found between rafted mussels in South Bristol and specimens obtained from the adjacent shore population. The total numbers of pearls within individual mussels in each year class are shown in Tables 11 and 12 for the raft and shore population, respectively. The regression lines and 95% confidence belts for the regression of the transformed $[\log(x+1)]$ counts on age are depicted in Figure 2 for each population. The regression equations for the raft and shore populations are, respectively,

$$Y = 0.1540X - 0.3765$$

and

$$Y = 0.1217X - 0.3266,$$

where Y is the estimated mean of the transformed $[\log(x+1)]$ pearl counts for a mussel of age X (in years). An estimate (\hat{Y}) of the mean number of pearls per mussel of age X is given in the following formula from Elliot (1971):

$$\hat{Y} = \text{antilog}[1.15 s_r^2 + Y] - 1,$$

where s_r is the standard error of Y for a given value of X . Following the procedure outlined by

TABLE 11. *The total number of pearls within individual mussels in each year class (raft).^a*

Specimen #	Raft (Number of pearls per individual)							
	Year Class							
	2	3	4	5	6	7	8	9
1	0	0	1	0	3	7	113	5
2	0	1	5	1	9	2	14	
3	0	0	1	0	1	1	3	
4	0	0	0	0		1		
5	0	0	0	1		2		
6	0	0	0	0				
7	0	0	1	7				
8	0	0	0	4				
9	0	1	0	1				
10	0	0	5					
11		1	0					
12		0	1					
13		2	1					
14		0	0					
15		0	0					
16		0	0					
17		0	0					
18		1	0					
19		0	4					
20		0						
21		0						
22		0						
23		1						
24		0						
25		0						
26		1						
27		0						
28		0						
Total	0	8	19	23	13	13	130	5
Mean	0	0.3	1.0	2.6	4.3	2.6	43.3	5.0

^aMussels were samples from a South Bristol rafted population.

Sokal and Rohlf (1969), an estimate of s_x for the raft and shore populations are provided by the equations

$$s_x = \sqrt{0.1521 \left[0.0128 + \frac{(X - 3.9872)^2}{1447} \right]}$$

and

$$s_x = \sqrt{0.0277 \left[0.0122 + \frac{(X - 5.4268)^2}{2739} \right]}$$

respectively. Once again, X is the age in years of

the specimen. Insertion of these estimates into Elliot's formula and substitution of the appropriate values of \hat{Y} for each population provides an estimate (\hat{Y}) of the mean number of pearls per mussel for both the raft and shore population. The equations are, respectively,

$$\hat{Y} = \text{antilog} (1.15 s_x^2 + 0.1540X - 0.3765) - 1$$

and

$$\hat{Y} = \text{antilog} (1.15 s_x^2 + 0.1217X - 0.3266) - 1$$

TABLE 12. The total number of pearls within individual mussels in each year class (shore).^a

Specimen #	Shore (Number of pearls per individual)								
	Year Class								
	2	3	4	5	6	7	8	9	
1	0	0	0	0	5	6	4	2	
2	0	0	1	0	8	0	9	3	
3	0	0	1	3	3	0	9	9	
4	0	0	0	1	1	0	9	4	
5	0	0	0	0	1	2	13	30	
6		1	0	0	1	6	0	6	
7		0	1	2	0	22	2	3	
8		0	0	0	30		1	1	
9		0	0	0	1				
10			0	0	3				
11			0	0	1				
12			3	4	0				
13			1	3	1				
14			4	0	0				
15			0	2					
16			0						
Total	0	1	11	15	55	36	47	58	
Mean	0	0.1	0.7	1.0	3.9	5.1	5.9	7.2	

^aMussels were sampled from a South Bristol shore population at the mean low water level.

However, in consideration of the relatively small magnitude of s_y^2 , the comparatively wide 95% confidence intervals, and the subjectivity associated with the counting of the annual lines on acetate peels, a relatively accurate estimation of Y for each population is provided by substitution of appropriate values in the equation

$$\hat{Y} = \text{antilog } Y - 1.$$

For both populations the linear regression on age was found to remove a highly significant portion of the variation of the transformed pearl counts (Table 13). The deviations from regression were not significant. Table 14 shows the results of the analysis of covariance comparing the two regression lines. No significant difference between the slopes of the regression lines nor between the adjusted transformed means of the two populations (elevation of lines) was detected in this study.

Finally, no pearls with diameters greater than 1 mm were found in mussels less than 5 years old. Two pearls (one from each population) with diameters greater than 1 mm were found in 5-year-old specimens.

DISCUSSION

The results of this study suggest that, with regard to the size and quantity of pearls in the mantle tissue, no difference exists between raft-based mussels and those of comparable age obtained from adjacent shore populations. The differences found between mussels of similar lengths obtained from rafts left for varying periods of time are probably a reflection of age differences between the individuals sampled. Similarly, the differences observed between raft and shore populations in this study are probably a reflection of a difference in the age distribution of specimens from the two environments. Lutz and Porter (1977) have shown that a 50 mm mussel is ob-

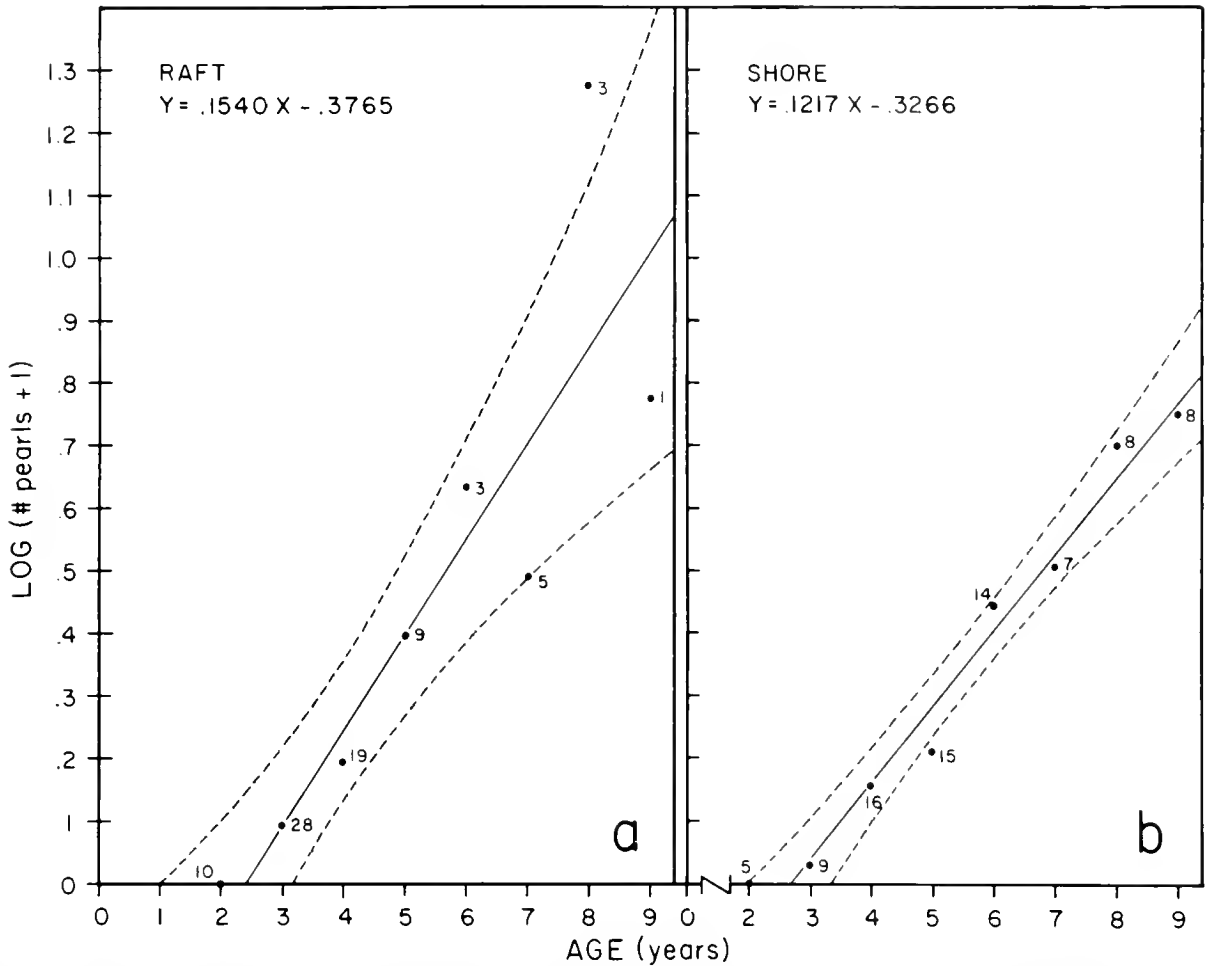


FIGURE 2. Regressions of logarithmically transformed pearl counts on age for raft and shore based mussels. Dashed lines represent 95% confidence belts.

tained in at least one Maine environment in a period of 12 months from settlement using rafting techniques. Reported estimates of the average growth rate of mussels (using length measurements) in natural populations (submerged and intertidal - the North Atlantic region) vary from 1.9 - 16.0 mm per year (Mossop, 1922a,b; Field, 1922). Thus, the rafting of mussels may increase linear growth rate as much as 3-25 fold over that of natural benthic populations. Therefore, although the age structure of the two population types (raft and shore) in most of the experiments conducted is not known, the average age of the shore mussels is suspected to be considerably greater than that of the rafted specimens.

If the rate of pearl formation and pearl growth

remains relatively constant throughout the life of a mussel, one might expect little or no difference between old and young individuals with regard to the number of pearls in the smallest size category. The results of Experiments #1 - #4 and the comparison of rafts left for varying lengths of time indicate that this is generally not the case. The greater number of small pearls in shore-based individuals and in mussels sampled from the rafts left longest in the water suggest that there is a general increase in the number of pearls being formed and/or a decrease in the growth rate of pearls as the individual ages. Both of these are probably occurring to some extent. As the individual ages, there is generally an increase in the surface area of the mantle epithelium. If, as has

TABLE 13. *Analyses of variance for regressions of transformed pearl counts on age.^a*

Raft				
Source of variation	df	SS	MS	F
Among year classes	7	5.8213	0.8316	12.3934**
Linear regression	1	4.9086	4.9086	32.2722**
Deviations from regression	6	0.9127	0.1521	2.2335 n.s.
Within year classes	70	4.7667	0.0681	
Total	77	10.5880		

Shore				
Source of variation	df	SS	MS	F
Among year classes	7	4.9670	0.7096	6.5945**
Linear regression	1	4.8010	4.8010	173.3213**
Deviations from regression	6	0.1660	0.0277	2.2574 n.s.
Within year classes	75	8.0720	0.1076	
Total	82	13.0590		

^aAn analysis is shown for each of two populations (raft and shore) in South Bristol, Maine.

**Indicates significance at the 0.01 level.

TABLE 14. *Analysis of covariance comparing the regressions of transformed pearl counts on age.^a*

Analysis of Covariance									
Transformed adjusted raft mean = 0.2375									
Transformed adjusted shore mean = 0.3338									
Within	df	χ^2	xy	y^2	b	df	SS	MS	F
Raft	77	206.9872	31.8750	10.5880	0.1540	76	5.6794	0.0747	
Shore	81	324.0610	39.4440	13.0390	0.1217	80	8.2379	0.1030	1.3788 n.s.
					Total	156	13.9173	0.0892	
Pooled, W	158	531.0482	71.3190	23.6270	0.1343	157	14.0490	0.0895	
					Difference between slopes	1	0.1317	0.1317	1.4765 n.s.
Between, B	1	82.8518	5.5404	0.3705					
		613.9000	76.8594	23.9976	0.1252	158	14.3749		
					Between adjusted means	1	0.3259	0.3259	3.6413 n.s.

^a The analysis compares the regression lines for two populations (raft and shore) in South Bristol, Maine.

been suggested by numerous workers (Garner, 1972; Dubois, 1901, 1909; Jameson, 1902; Jameson and Nicoll, 1913), pearl formation is a result of trematode infection, this increased surface area may offer a greater number of sites for penetration by the parasite, and, hence, would result in an increased number of pearls. As the majority of pearls in *M. edulis* are nacreous, the same

processes controlling thickening of the inner shell layer may control the growth of pearls. This was recognized by Jameson (1902, p. 161) who stated in reference to pearls, "their growth is, in fact, regulated by the causes which control the thickening of the shell." Examination of the polished shell sections and corresponding acetate peels presented by Lutz (1976) reveals that there is a general

decrease in the width of annual increments with increasing age of the specimen. A similar decrease in the growth rate of pearls probably occurs.

Jameson (1902) and Nicoll (1906) claim that the gymnophallid trematode responsible for pearl formation in *M. edulis* from French and English waters enters the mussel as a tailless cercaria. This, in turn, led Jameson (1902, p. 160) to conclude that "in order to be abundantly infected, *Mytilus* must be on the bottom." Dubois (1909) disagrees, claiming to have found all larval stages of the trematode within the mantle of *M. edulis*. If pearls in mussels from Maine waters are also a result of infection by the trematode, *Gymnophallus*, the results of the present study appear to discredit the claims of Jameson (1902) and Nicoll (1906). If a larval stage of *Gymnophallus* enters *M. edulis*, it is a stage that is not restricted to a bottom habitat.

Dubois (1907b) conducted an experiment to test the effect of increased temperatures on the metamorphosis of metacercariae larvae of the gymnophallid trematode responsible for the initiation of pearl formation. Based on the acquisition of adult characteristics at higher temperatures (35 - 40°C), he concluded that larval metamorphosis to the adult form must take place in a warm-blooded animal. Jameson and Nicoll (1913) suggest that the common eider duck, *Somateria mollissima*, and/or the black scoter, *Oidemia nigra*, serve(s) as the definitive host(s). Stunkard and Uzman (1958) fed metacercaria-infected mussels from Long Island to newly hatched eider chicks and recovered adult gymnophallids, probably *G. bursicola* (Odhner, 1905), from the intestines of the chicks. Both *Oidemia nigra* and *Somateria mollissima* are abundant in certain areas throughout the Gulf of Maine and either one or both may serve as the adult host(s) for this trematode. If pearl formation in these waters is a result of gymnophallid infection, it is reasonable to expect the presence and quantity of pearls in mussels to be somewhat correlated with the presence and abundance of eiders and/or scoters in the surrounding waters. Before such a correlation can be made, however, age-independent differences (if existent) in pearl incidence between geographically isolated populations of *M. edulis* must be quantified. The results of this study sug-

gest a method of obtaining such quantification.

Several workers (Jameson, 1902; Nicoll, 1906; Lebour, 1906) have suggested that a second intermediate host may be required for completion of the life cycle of the trematode responsible for pearl formation. Jameson (1902) found sporocysts containing larvae, almost identical with those which occur in *M. edulis*, within the mantle margins of the bivalves, *Tapes decussatus* and *Cardium edule*. Nicoll (1906), in his examination of numerous specimens of *Cardium edule*, failed to find such sporocysts in the mantle margin, but noted (P. 149) their frequent occurrence in "one well-defined, somewhat oval-shaped mass situated in the middle line dorsally just over the posterior border of the liver." Neither *Tapes decussatus* nor *Cardium edule* are found within the Gulf of Maine. Thus, if the trematode (probably *Gymnophallus bursicola*) responsible for the initiation of pearl formation in Maine waters requires a second intermediate host for the completion of its life cycle, such a host remains to be found. Furthermore, if this trematode is responsible for the initiation of pearl formation in Maine waters and if one and only one additional intermediate host is required, the presence and quantity of pearls in mussels should be correlated with the distribution patterns of this host. Again, the results of this study suggest a method of quantifying differences (independent of age) between geographically isolated *M. edulis* populations with regard to pearl incidence, facilitating correlation of the presence and quantity of pearls with the presence and abundance of such a host.

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BLUE CRAB PREDATION ON CULTCHLESS OYSTER SPAT

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ABSTRACT

Many cultchless oyster spat (*Crassostrea virginica*) planted experimentally on natural bottoms in Maryland portions of the Chesapeake Bay in 1975 and 1976 have been destroyed by blue crabs (*Callinectes sapidus*). High mortalities (70 to 90%) were observed within one month after oysters ranging from (3 mm-40 mm) in diameter were placed directly on natural bottom or in trays without closed tops. Oysters in enclosed trays at these locations exhibited no unusual mortality. Several patterns of shell destruction (chipped shell edges, a single puncture over the adductor muscle, broken area of original spat attachment and opposing notches on the shell edges) were observed among the oyster shells collected from the field. The same destruction patterns were observed when cultchless oyster spat were placed in aquaria containing adult blue crabs. Cultchless oyster spat which produce high quality half-shell oysters if grown in protected containers, may be of little value when planted on natural bottom in Maryland to sustain native oyster stocks, or to obtain an economical return from a planted private lease.

INTRODUCTION

Crabs of various species are important predators on oyster spat. Stone crabs (*Menippe mercenaria*) are a serious problem in the States bordering the Gulf of Mexico. So are green crabs (*Carcinus maenas*) and mud crabs (*Neopanope texana*) in New England states (Galtsoff, 1964). Mud crabs were incriminated in very high mortalities (as high as 50 percent) of Connecticut oyster spat less than 10 mm long by MacKenzie (1970). Several authors have also noted that the blue crab, *Callinectes sapidus*, can cause high levels of mortality in natural oyster and clam populations in the Middle Atlantic and Gulf States (Lunz, 1947; Menzel & Hopkins, 1955). Menzel &

Hopkins (1955) observed the feeding behavior of blue crabs in floating cages and found that a single crab can consume up to 19 oyster spat per day.

Castagna (1970) suggests that predation by blue crabs is the major constraint in the culture of hard clams on natural bottoms. Without some form of protection, clam mortality can approach 100 percent (Menzel et al, 1976; Castagna et al, 1970).

The same constraint — predation by crabs — has been encountered in our attempts to grow cultchless oyster spat on the natural bottom in the Chesapeake Bay. It is obvious that large populations of blue crabs in our coastal waters could completely neutralize oyster mariculture operations, especially if spat are too small when planted or if the spat are not protected. We have planted

cultchless oyster spat of various sizes to determine the optimum size at which to plant hatchery-reared spat and to insure enough survival for a positive economic return from the cost of the spat.

FIELD STUDIES

Our studies were conducted on the upper Eastern Shore of the Maryland portion of the Chesapeake Bay. Mean annual salinity of this region ranges from 8 to 12 ppt. This area has no significant populations of oyster drills, *Urosalpinx cinerea* and *Eupleura caudata*. The most probable predators on oyster spat in this region are the flat worm, *Stylochus ellipticus*; the mud crab, *Rithropanopeus harrisi*; the blue crab; and some fish species: oyster toadfish, *Opsanus tau*; croaker, *Micropogon undulatus*; spot, *Leiostomus xanthurus*; cow-nosed ray, *Rhinoptera bonasus*.

Our first planting study utilized 4 1/10 acre plots on hard sandy bottom. The bottom had very little habitat for mud crabs or other members of the oyster bed community. The plots were planted with 125,000 cultchless spat in late September, 1975, each plot receiving oysters of 1/2", 1 1/2", 3/4" and 1" (6mm, 12 mm, 20 mm, 25 mm) in length. The spat were produced by the Dupuy (1973) technique, were removed from Mylar sheets when they were about 1/2" (5 to 15 mm), and grown in fiberglass trays in the hatchery until planted.

After two weeks on the bottom, the spat were observed by scuba divers. All of the 6 mm spat were missing and very little shell remained. Mortality in the other plots ranged from 30 to 60 percent in sample locations. By the following spring (May 1976) no live oysters could be found. All of the recovered shells had broken margins with large portions of the shell missing. We thought severe storm conditions might have tumbled the shells on the bottom, broken the edges of the shell and killed the oyster spat.

In 1976 ten different locations where the bottom was protected from wave action were planted with clutchless spat.

One such area was planted in July with cultchless oysters ranging from 19 to 38 mm long. Ten thousand spat were planted on a 100 sq. ft. area marked by stakes on an active commercial oyster bed. Within two weeks, all the clutchless spat were dead. Blue crabs were observed to be

abundant at this location whereas mud crabs were not found. Broken shells from the clutchless spat were found in the planted area.

In another location, trays of cultchless oysters ranging from 3 to 40 mm in length were placed adjacent to a natural oyster bar. Half the trays had fine-mesh wire tops, while half were unprotected. Within one month 99.7 percent of the unprotected cultchless spat were dead, while the protected had no detectable mortality. The shells of the dead spat had the same type of damage that was observed at previous planting locations.

These are two of the most severe cases of predation we have observed but significant losses were incurred at other planting sites even though spat were planted in early November, 1976, after most blue crabs had become dormant.

PATTERNS OF SHELL DAMAGE BY THE BLUE CRABS

To confirm the hypothesis that blue crabs were involved in the losses of oysters in the field we fed cultchless oysters of various sizes to crabs in aquaria. Blue crabs from 4" to 6" (100 mm to 150 mm) carapace width were found to be capable of consuming cultchless oysters up to 40 mm in length. Blue crabs from 65 mm to 80 mm in carapace width were unable to consume cultchless oysters larger than 1" (25 mm) in length.

Methods used by blue crabs to break oyster shells vary from oyster to oyster. Small oyster spat (3 mm to 15 mm) were simply crushed and the meat separated from shell as the oyster was eaten. Frequently the entire crushed oyster was ingested and no shell fragments could be found.

The next most common feeding strategy was to chip the shell margin with the chelae so that the mouth parts and chelae tips could extract the oyster meat. Figure 1 is a scale drawing to show this type of damage. Note that the spat shell has very irregular edges and most of the recent shell growth was removed, often in large chips. These oysters look as if they had been damaged by tumbling along a hard bottom. This was the predominant pattern of damage observed in our 1975 bottom planting of cultchless oysters.

A characteristic of cultchless spat produced by the Dupuy mylar technique is thinness of the shell over the area where the lower valve of the spat

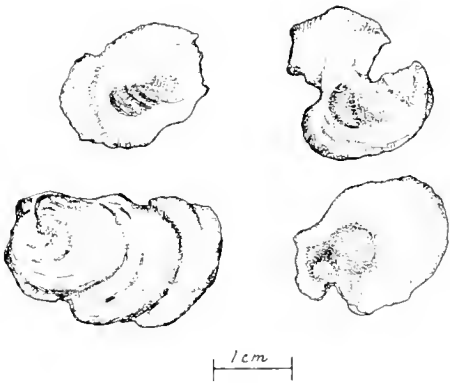


FIG. 1. Shells of cultchless oyster spat showing blue crab damage to shell margins.

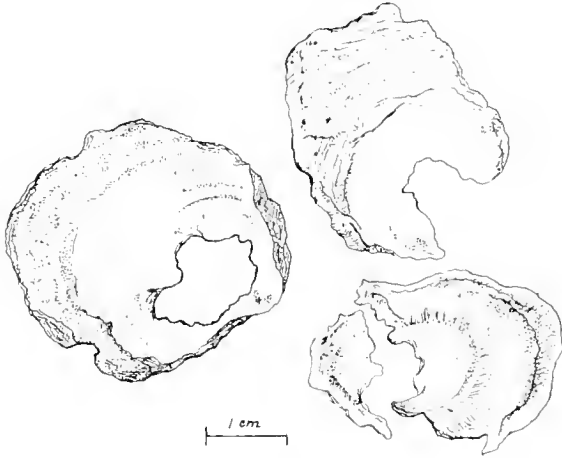


FIG. 2. Shells of cultchless oyster spat showing blue crab damage to soft, flattened areas produced on lower valves by the Mylar technique of spat collection.

was attached to mylar. This area is easily broken by the human fingernail and contributes to mortality while handling small spat in oyster hatcheries. Blue crabs frequently crushed this area (Figure 2) in their attempts to open the cultchless oysters. Another approach was to crush the umbo, or hinge area (Figure 3), which then permitted the crab to extract the oyster meat. A fairly common type of observed damage was the removal of large chips from opposite sides of the oyster shell as if the crab compressed the shell laterally between the digits of the chelae (Figure 4).

The most puzzling damage we observed in the planting studies, were spat with a single round hole in the shell (Figure 5). Up to 10 percent of the

shells in some samples had this type of damage. Initially we thought that another predator was involved in the losses of the hatchery-reared spat. However, feeding studies in the laboratory showed that blue crabs were quite effective at punching holes. Occasionally we found shells which had multiple holes. Figure 5 shows that the holes are not round but are slightly irregular. Frequently the inner shell surface of the hole and the "walls" showed irregular fractures on the margins. The damage differs from the more regular, smooth and slightly conical holes made by oyster drills.

Perhaps the most important observation made during the study was that to damage the cultchless oyster spat all that was required was that blue

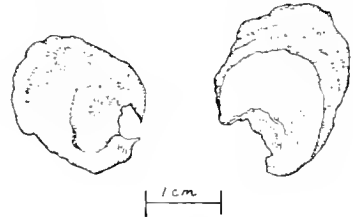


FIG. 3. Shells of cultchless oyster spat with umbo area crushed by blue crabs.

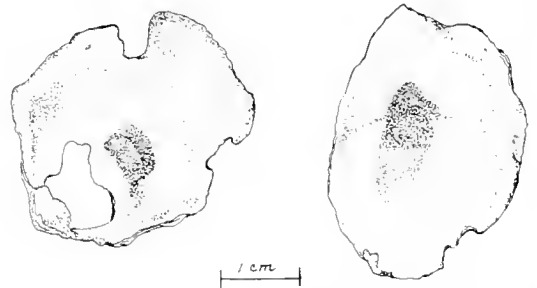


FIG. 4. An example of chips removed by blue crabs from opposite edges of cultchless oyster shells.

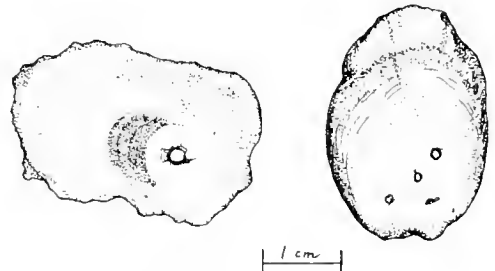


FIG. 5. Holes punched through the shell of oyster spat by blue crab.

crabs pick up and manipulate the oyster spat in their claws. In this situation the edges of the cultchless spat were accessible, in contrast to spat on oyster shell cultch. The fragile shell edges of cultchless oysters were easily chipped even by small blue crabs and clutchless spat were easily manipulated to the mouth of the crab.

Laboratory feeding studies showed that blue crabs had much greater difficulty manipulating a large piece of cultch to which oyster spat were attached. Frequently the crab's claws were unable to contact the spat in a manner that would damage the shell. Manipulation to the mouth was definitely impaired by cultch of any size.

MacKenzie (1970) noted that mud crabs in Connecticut rarely attacked an attached spat over 10 mm (about 1/2 in.) but they readily consumed unattached spat up to 25 mm. His field observations were confirmed by our laboratory studies.

Our present mariculture strategy is to determine what size of spat on various types of cultch best survives the blue crab predation in Maryland portions of Chesapeake Bay. Hopefully a combination of cultch type, size of cultch, and size of oyster spat can be found that will reduce mortality to a level where a positive economic return can be realized from planting hatchery-reared spat on the natural bay bottom.

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The authors wish to acknowledge Dr. John Dupuy for culturing some of the oysters used in this study, Donald Meritt for assistance in field work and for oysters he raised for the study, and Mrs. Deborah Kennedy for her drawings of damaged oyster spat.

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PREDATION ON HARD CLAMS,
MERCENARIA MERCENARIA,
BY MUD CRABS, *PANOPEUS HERBSTII*¹

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ABSTRACT

Predation on hard clams planted in protected trays was studied by examination of empty clam shells and the stomach contents of potential predators gaining entry to the trays. Decapod crustaceans comprised 88.5% of the predators collected. Panopeus herbstii was the most abundant species while Callinectes sapidus and Menippe mercenaria were only occasionally found. Gastropods were collected, but examination of empty clam shells revealed no evidence of gastropod predation. Stomach analysis revealed clam shell bits in four crab species. Shell bits were found in 15.8% of the 279 P. herbstii analyzed. Occurrence of shell bits varied but were more often found in stomachs of larger crabs.

The abundance and mean size of P. herbstii in trays varied from a peak in summer to a low in winter. Clam mortalities decreased with increases in clam size and with decreases in water temperature. Frequency of shell bits in the stomachs of P. herbstii paralleled clam mortality. Some size selection process appeared to be operating in this predator-prey system.

INTRODUCTION

The potential exists for improving the hard clam, *Mercenaria mercenaria*, industry in South Carolina. Rapid growth of clams, vast amounts of suitable tidelands, increased market for southern clams, and recent success of the Santee fishery are some of the reasons for this optimism (Eldridge, Waltz, Gracy and Hunt, 1976; Gracy, 1974; Gracy and Keith, 1975). Clam mariculture has also been demonstrated to be feasible in pilot studies in Virginia (Castagna, Mason and Briggs, 1970), but more work remains to be done. A major problem in culturing clams is predation. The

objectives of this study were to investigate predation in protected trays in an estuary in South Carolina and to identify some important factors influencing predation.

MATERIALS AND METHODS

Hatchery clams (\bar{X} = 13 mm shell length, SL) were planted in 20 protected oyster trays (10 intertidal, 10 subtidal) containing natural sediment in May, 1975. Basket compartments (118 x 61 x 14 cm) in the trays were enclosed with 9 mm plastic netting and lined with fiberglass insect screens to retain sediment. Each tray was covered with 9 mm plastic netting to help protect against predation. This was not completely successful because potential predators apparently could enter trays

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through the crack between the cover and basket compartment. The trays were located near Clark Sound, S. C. (Lat. 32° 42' 5" N, Long. 79° 52' 2" W) in an area characterized by a soft sand (20-30% silt-clay) bottom and a salinity range of 25-30‰ at low tide.

Fifteen collections of potential predators were made from May, 1975 to December, 1976. All potential predators were saved except for the collections in June and July, 1975, when representative samples were taken from each tray. Members of other feeding groups (e.g. filter feeding polychaetes) were not collected. Field collections were preserved in 10% formalin until specimens could be sorted and counted. Crustaceans were sexed and measured to the nearest 0.1 mm. The stomach contents of each crustacean and, in most cases, all the specimens collected were examined to determine the food types. Samples of the abundant crustaceans, *Panopeus*

herbstii and the snapping shrimp (*Alpheus* spp.), were selected for examination. Samples of *P. herbstii* included representatives from each sample date, tidal location, and three class intervals of carapace widths (CW): small crabs ≤15 mm CW; medium crabs 15.1-25.0 mm CW; and large crabs >25 mm CW. Cardiac stomachs were excised, and the individual food items were sorted as clam shell bits, arthropod parts, plant material and grit. Finely ground food items which could not be identified and sediment were classified as grit. The frequency of each food item was expressed as percent occurrence in individuals containing food. The quantity of a food item was estimated by the 'points' method (Hynes, 1950).

Clam growth and mortality in each tray was determined during the sampling period. Clam density was maintained in the individual trays by replacing dead or sacrificed clams with marked clams of comparable size. Empty clam shells were

TABLE 1. Potential predators collected from 20 protected trays containing clams. Numbers and percentages represent totals for 15 sampling dates from 5/75 through 12/76. The presence of clam shell bits in stomachs is represented by +; the absence 0 and not examined ne.

	Number	% of Order	% of Class	% of Total	Presence Clam Shell Bits
CRUSTACEA	1746	—	100.0	88.9	+
Decapoda	1740	100.0	99.7	88.5	+
<i>Panopeus herbstii</i>	1465	84.2	83.9	74.6	+
<i>Callinectes sapidus</i>	8	0.5	0.5	0.4	+
<i>Menippe mercenaria</i>	8	0.5	0.5	0.4	+
<i>Eurypanopeus depressus</i>	13	0.7	0.7	0.7	+
<i>Neopanope texana</i>	2	0.1	0.1	0.1	0
<i>Uca pugnator</i>	9	0.5	0.5	0.5	0
<i>Eurytium limosum</i>	2	0.1	0.1	0.1	0
<i>Pachygrapsus transversus</i>	1	0.1	0.1	0.1	0
<i>Alpheus heterochaelis</i>	184	10.6	10.5	9.4	0
<i>Alpheus armillatus</i>	39	2.2	2.2	2.0	0
<i>Alpheus normanni</i>	9	0.5	0.5	0.5	0
Stomatopoda	6	100.0	0.3	0.3	0
<i>Squilla empusa</i>	6	100.0	0.3	0.3	0
GASTROPODA	219	—	100.0	11.1	ne
Neogastropoda	219	100.0	100.0	11.1	ne
<i>Urosalpinx cinerea</i>	150	68.5	68.5	7.6	ne
<i>Nassarius vibex</i>	10	4.6	4.6	0.5	ne
<i>Nassarius obsoleta</i>	56	25.6	25.6	2.8	ne
<i>Eupleura caudata</i>	3	1.4	1.4	0.2	ne
TOTAL	1965				

collected to determine the size of dead clams and possible cause of mortality. Materials and methods not detailed above were described previously (Eldridge et al., 1976).

RESULTS

The number of potential predators found in the trays are presented in Table 1. *P. herbstii*, a mud crab, was the most abundant (75%) species collected. Predators of clams which are generally suspected, *Callinectes sapidus* and *Menippe mercenaria*, comprised less than 1% of the specimens found. Gastropods were common, but empty clam shells did not exhibit the borehole characteristic of gastropod predation. Cracked and crushed clam shells were abundant in the trays indicating forced entry, probably by crustaceans.

Fourteen percent of the 362 crustaceans examined contained clam shell bits in their cardiac stomachs. Only four species (i.e., *P. herbstii*, *C. sapidus*, *Menippe mercenaria* and *Eurypanopeus depressus*) of the 12 species of crustaceans examined contained shell bits (Table 2). There was no significant difference ($P > 0.05$) between the occurrence of shell bits in the four species.

Clam shell bits were more frequent in stomachs of large crabs (Table 2). Shell bits were found in significantly greater ($P < 0.05$) percentage of large *P. herbstii* than were found in medium and small ones. Although percent occurrence of shell bits in *P. herbstii* were significantly different between sizes, volumes (i.e. point method) were not. Variation in this trend among the less abundant species can be accounted for by the number and temporal differences of the crab populations in the trays. No shell bits were observed in medium-sized *E. depressus* (15.1-25.0 mm CW), however crabs this size were absent until May, 1976 when clams had a 36.6 mm mean shell length. Small sample sizes also limited statistical analyses of data on the less abundant species.

Prey size, as well as predator size, apparently affects clam mortality levels. The mean shell lengths (SL in mm) of live and dead clams (i.e. empty shells) increased linearly after time of planting (x = time in months). The regressions are:

$$\begin{aligned} \text{live clams} & \quad \times \text{SL} = 1.69x + 4.76; \text{ and} \\ \text{dead clams} & \quad \times \text{SL} = 1.31x + 3.37, \end{aligned}$$

with r values of 0.99 and 0.96 respectively. These linear regressions are significantly different

TABLE 2. Analysis of crab stomach contents containing clam shell bits. Percent occurrence is based on those crabs with food. Crab size class intervals are small ≤ 15.0 mm carapace width (CW), medium 15.1-25.0 mm CW and large > 25.0 mm CW.

Crab Species	Carapace Width	Number Examined	Food	Clam Shells	% Occurrence		Grit
					Arthropods	Plants	
<i>Panopeus herbstii</i>	Small	92	76.1	10.0	20.0	44.3	100.0
	Medium	119	87.4	15.4	18.3	38.5	100.0
	Large	68	97.1	31.8	31.8	43.9	100.0
	Total	279	86.0	18.3	22.5	41.7	100.0
<i>Callinectes sapidus</i>	Small	3	100.0	0	0	33.3	100.0
	Medium	1	100.0	0	0	0	100.0
	Large	4	100.0	50.0	50.0	25.0	100.0
	Total	8	100.0	25.0	25.0	25.0	100.0
<i>Menippe mercenaria</i>	Small	7	71.4	20.0	40.0	20.0	100.0
	Large	1	100.0	100.0	0	0	100.0
	Total	8	75.0	33.3	33.3	16.7	100.0
<i>Eurypanopeus depressus</i>	Small	4	100.0	25.0	0	50.0	100.0
	Medium	6	83.3	0	0	40.0	100.0
	Large	3	100.0	66.7	33.3	66.7	100.0
	Total	13	92.3	25.0	8.3	50.0	100.0

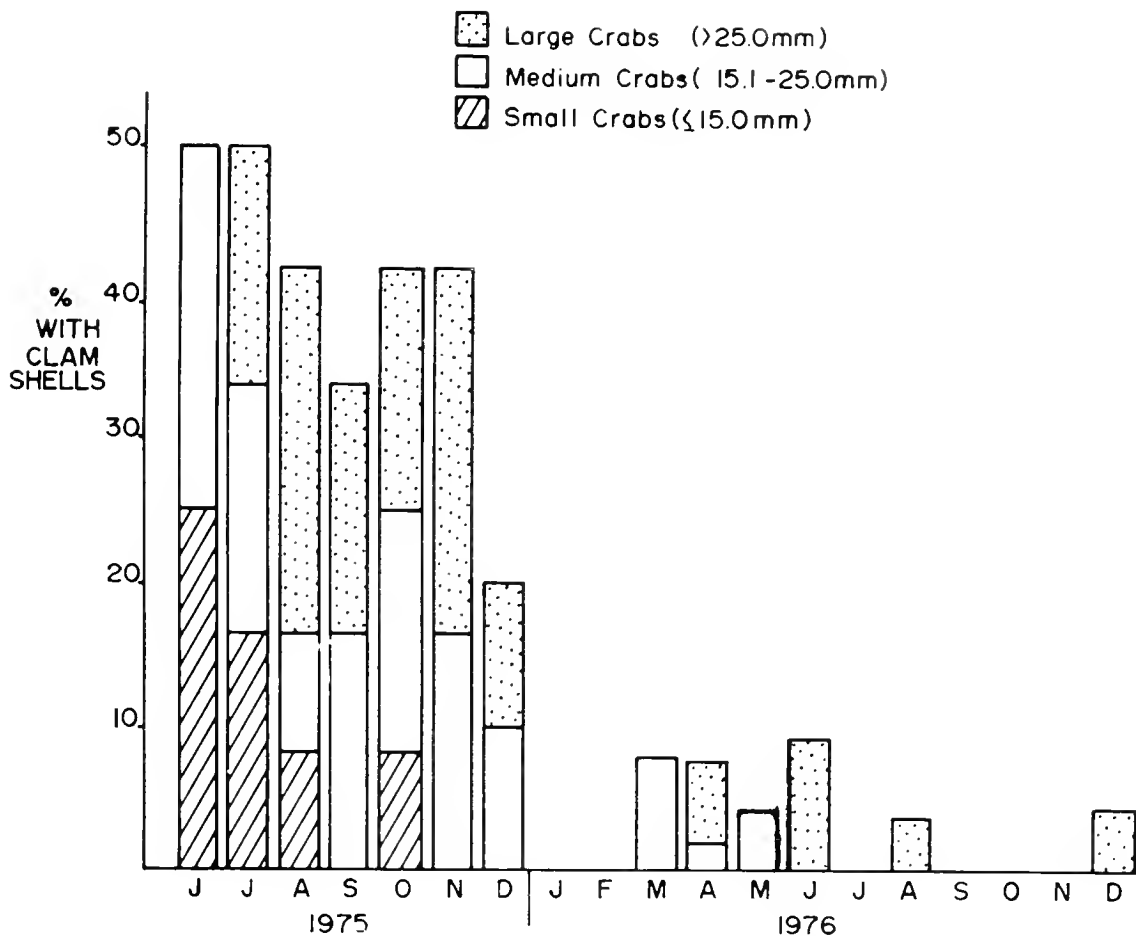


FIGURE 1. Percent *P. herbstii* containing food with clam shell bits plotted against sampling month. At any date the percentage of crabs containing food with shell bits is represented by the entire histogram. Representatives of each size class interval were found in all collections except 1975 when no large crabs were found.

($P < 0.01$) suggesting clam size as an integral component of predation. As clam size increased the percentage of *P. herbstii* containing clam shell bits decreased (Figure 1). Also the proportion of large *P. herbstii* with shell bits increased from 40% in 1975 to 67% in 1976. Only large *P. herbstii* contained shell bits one year after planting. Over the same period, mortality of clams decreased from a high of 30.2% to a relatively constant low mortality of approximately 0.5% per month by March, 1976. (Figure 2).

The abundance and mean size of *P. herbstii* varied throughout the experimental period (Figure 3). This variation could be due to several cohorts

in the crab population. The mean size of crabs was greatest in the warmer months (i.e. June - October). Laboratory observations indicate that in *P. herbstii* 20.0 mm CW was the minimum size necessary for successful predation upon clams above 11.5 mm SL (the approximate planting size). The percentage of the crab population above this minimum successful predator size changed significantly ($P < 0.05$) throughout the year with the greatest percentage in the summer (i.e. June, July, and August). Also the average number of *P. herbstii* above 20 mm CW was significantly ($P < 0.05$) greater during the summer than fall, winter and spring. This seasonal variation of *P.*

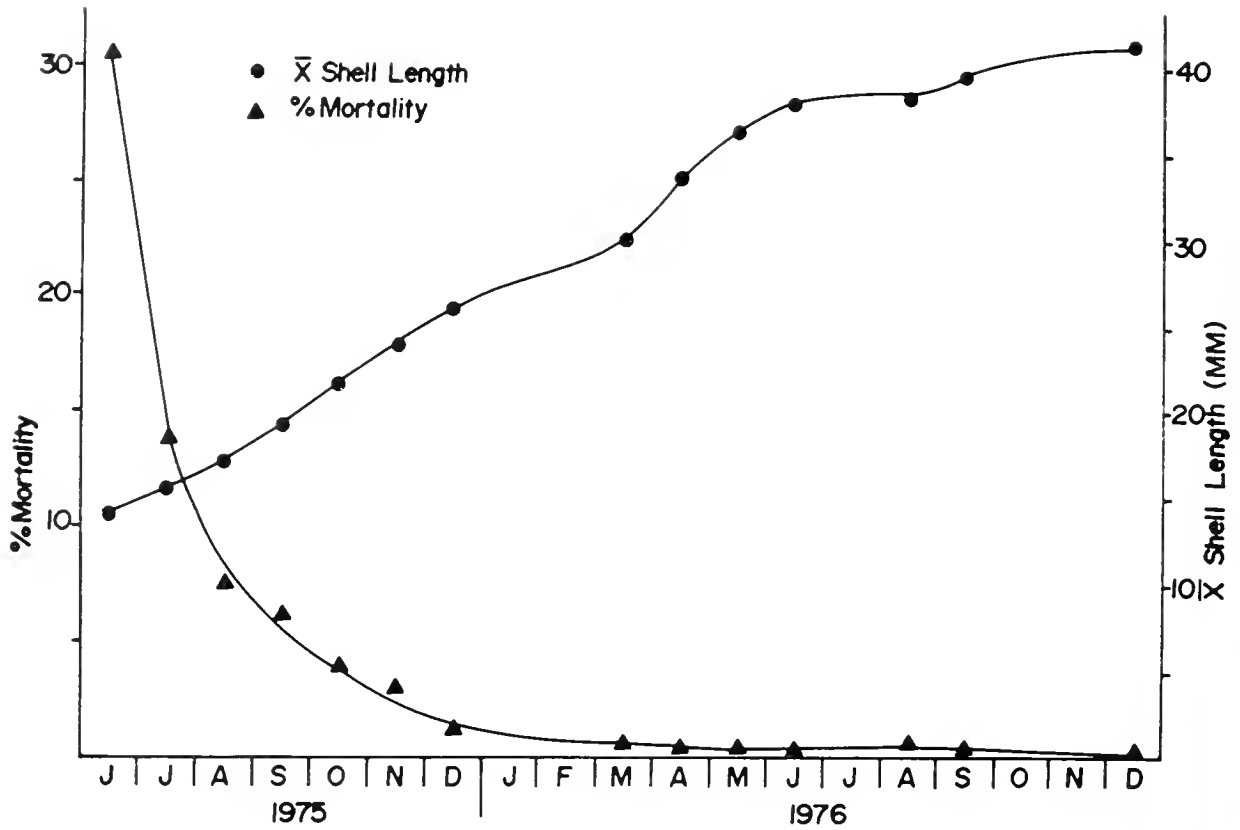


FIGURE 2. Percent mortality of clams and mean shell length of live clams grown in 20 protected trays plotted against sampling date. (P. J. Eldridge and A. G. Eversole, unpublished data).

herbstii allows speculation into some methods of predator control.

DISCUSSION

Callinectes sapidus, *Carcinus maenas*, and *Menippe mercenaria* have been documented as major predators of the hard clam, *Mercenaria mercenaria* (Belding, 1912; Carriker, 1951; Godwin, 1968; Haven and Andrews, 1957; Loosanoff, 1946; Menzel, Cake, Haines, Martin and Olsen, 1976; Menzel and Sims, 1962). *Callinectes sapidus* and *Menippe mercenaria* have been suspected of causing 100% mortality in hard clams planted in unprotected plots in Georgia and Florida (Godwin, 1968; Menzel and Sims, 1962). Haven and Andrews (1957) reported *C. sapidus* as the major predator of hard clams planted in suspended trays in Virginia. Other decapods have been proposed as predators of hard clams. Eldridge et al. (1976) suggested mud crabs, members of the Xanthidae

family, were important predators of clams in South Carolina.

Callinectes sapidus and *Menippe mercenaria* comprised less than 1% of the potential predators collected and could not be the major cause of mortality in our culture system. Clam shell bits were found in only four species of predators, three of which were xanthid crabs. The xanthid crab, *P. herbstii*, appeared to be the most important predator in this system. To date no specific mention has been made of *P. herbstii* as a predator of the hard clam, although McDermott (1960) cited a predator-prey interaction between *P. herbstii* and *Crassostrea virginica*. Carriker (1959) and Landers (1954) also cited *Neopanope texana* a xanthid crab, as an effective predator of seed clams.

Prey and predator size appear to be major factors in the *Panopeus herbstii* - *Mercenaria mercenaria* interaction. Menzel and Hopkins

(1956) observed that the size of the *Menippe mercenaria* limits this xanthid crab's ability to prey on oysters. Our findings indicate that larger *P. herbstii* preyed more successfully on clams than smaller crabs. Also, the proportion of small and medium crabs containing clam shell bits decreased as clam size increased. A major decline in mortality was observed as clams grew larger, and the percent of *P. herbstii* containing shell bits declined from 50% when clams averaged 15.5 mm SL to less than 5% after clams reached an average size of 38.4 mm SL. Carriker (1959) observed that a larger initial planting size significantly reduced mortality of clams in unprotected plots. Assuming that predatory activity of *P. herbstii* was limited by clam size, planting larger clams should reduce mortalities.

Crabs may be selecting the smaller clams in the trays. The regression for mean shell lengths of live clams against time (months) was significantly greater than the regression for the mean shell lengths of dead clams. Furthermore this regression for live clams was significantly greater than a regression representing the projected sizes of dead clams if the dead clams had the opportunity to grow throughout each sampling interval. The projected size was computed by adding the mean shell length of dead clams and an increment equivalent to shell growth of live clams for the appropriate sampling interval. McDermott (1960) suspected that *P. herbstii* selected thinner-shelled oysters. Cake (1970) found no prey size selectivity by *C. sapidus* and *Menippe mercenaria* when offered sunray venus clams, *Macrocallista nimbosa*. Smaller species of crabs may not have the ability to open the larger and/or thicker-shelled molluscs. Smaller species of crabs such as *P. herbstii* may therefore exhibit more prey size selection than larger crab species. If the larger crabs are more capable of preying on a wide variety of clam sizes or thicknesses, then prey size selectivity probably will not be pronounced. This may explain, in part, why Cake (1970) observed no size selectivity with *C. sapidus* and *Menippe mercenaria*.

Menzel and Hopkins (1956) found lower mortalities in oysters in Louisiana during the winter, and predation by *Menippe mercenaria* was not observed below 10°C. Similarly we observed lower mortalities in the winter months when water

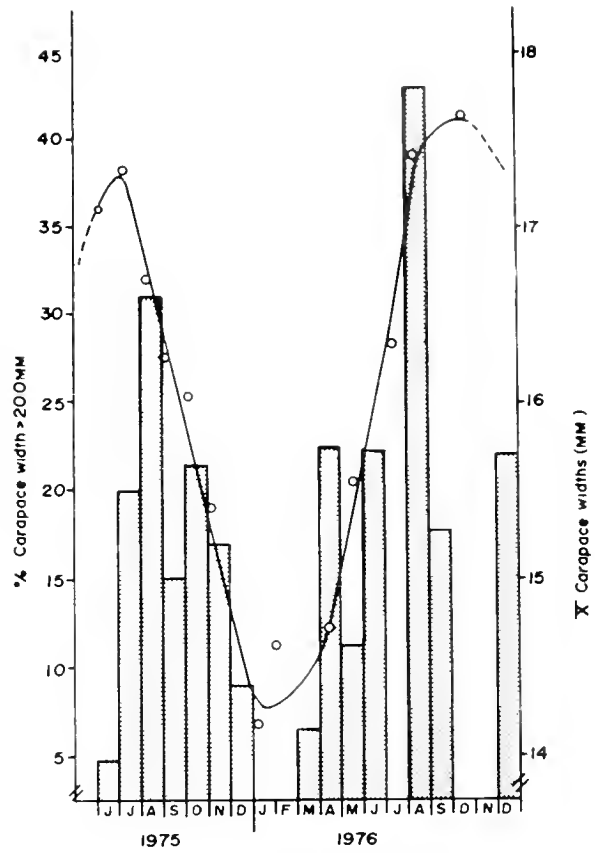


FIGURE 3. Smoothed means of carapace widths (in mm) of *P. herbstii* from trays plotted against mean sampling dates. Histograms show percentages of sampled crabs with carapace widths larger than 20 mm.

temperatures approached 8°C. Less activity by the crabs in the winter would contribute to this lower observed mortality. Lower mortality also corresponded to the presence of fewer *P. herbstii* and a smaller percentage above the minimum effective predator size during winter.

Time of planting and clam size should be considered in formulating any management program for extensive clam culture operations. Planting clams in the late fall should improve survival of seed because predator populations are then at lower levels. Also, there are fewer large predators, and predators are generally less active during cooler months. In addition, during this period clams have an opportunity to grow to a size that

will limit predation by the smaller crabs. If selected planting times and clam sizes were used with other techniques such as aggregate protection to effectively reduce predation, clam culture can be successful and profitable even in areas where predators abound.

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SEASONAL ASPECTS OF THE BIOLOGY, DISTRIBUTION AND
RELATIVE ABUNDANCE OF THE DEEP-SEA RED CRAB
GERYON QUINQUEDENS SMITH, IN THE VICINITY OF THE
NORFOLK CANYON, WESTERN NORTH ATLANTIC^{1, 2}

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ABSTRACT

Deep-sea red crabs were collected from demersal trawl surveys of Norfolk Canyon and an adjacent open slope area in the Chesapeake Bight of the western North Atlantic Ocean. The surveys were made in each of four seasons over a period of three years. The 2539 red crabs caught ranged from 16mm to 143 mm in carapace length (CL). Relationships between CL and carapace width (CW) were derived for 308 males and for 269 females. Wet weight to CL relationships were derived for 238 males and for 142 females.

Red crabs were contagiously distributed within the total depth range of capture (200-1800m) as well as within the 300-1000 m range of most consistent catches. They were equally abundant in canyon and slope regions in the four seasons. The majority of the population inhabits bottom water deeper than 400 m and overlain by cold, well-oxygenated water.

Over 50% of all red crabs were larger than 96 mm CL (114 mm CW), the minimum size presently acceptable to processing plants. This proportion varied by sex, season and depth. Potentially marketable male crabs constituted 70% of total males caught, whereas less than 25% of females exceeded 96 mm CL. Seasonally the proportions were consistent for males, but varied for females. The proportion of large males was consistent over most of the depth range (200-1600 m). Most of the larger females were captured in water shallower than 600 m.

An inverse relationship between water depth and crab size was evident for females from 200-1500 m; for males only in the 200-500 m depth range. The mean size of males caught deeper than 600 m was fairly stable.

Females were more abundant than males in samples shallower than 600 m; males dominated catches in deeper water.

A spawning cycle is suggested although ovigerous females were captured in all seasons. Peak incidence of ovigerous females occurs in November characterized by a high percentage of late stage eggs and a peak incidence of recently extruded eggs. The

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ovarian cycle of non-ovigerous females complements the spawning pattern. From June through November, an increase in incidence of developing ovaries was accompanied by a decrease in advanced and mature ovaries. Absence of mature ovaries in November complements the peak incidence of ovigerous females at that time.

Relative density of red crabs was estimated for the Norfolk Canyon area and compared with values from other areas along the east coast of the United States.

INTRODUCTION

Interest in *Geryon quinque-dens* Smith as a marketable species has been slowly increasing. Initial explorations (Schroeder 1959; McRae 1961) proved that red crabs were readily captured with trawls off the east coast of the United States. More recent surveys have been concerned with estimating fishery potential and evaluating harvesting methods, both in the United States (Gray⁴; Haefner and Musick, 1974; Ganz and Hermann⁵; Wigley, Theroux and Murray, 1975) and in Africa (Dias and Machado⁶; LeLoeuff, Intes and LeGuen, 1974; Intes and LeLoeuff, 1976). Technological and economic aspects of harvesting have also been under investigation (Varga, Dewar and Anderson, 1969; Meade and Gray, 1973; Holmsen and McAllister, 1974).

Other than the data obtained by Haefner and Musick (1974) and Wigley, et al. (1975), which were restricted to one period of sampling, observations on the biology of *Geryon* have been superficial. This paper supplements the survey of Haefner and Musick (1974) by presenting seasonal data on distribution, relative abundance and reproductive biology of red crabs in the Chesapeake Bight area of the western North Atlantic Ocean.

MATERIALS AND METHODS

Deep-sea red crabs were collected during demersal fish trawl surveys of Norfolk Canyon and an

adjacent open slope area in the Chesapeake Bight region of the western North Atlantic Ocean (Figure 1.) Four surveys, one in each season, were made during a period of three years using University of Miami vessels R/V *Columbus O. Iselin* and *James M. Gilliss* (Table 1). The sampling gear consisted of 15.1 m (headrope) semi-balloon, 4-seam shrimp trawls equipped with plastic mud-rollers and steel China V-doors. The nets were nylon of the following stretch mesh: 44 mm body, 37 mm intermediate, 36 mm codend and 12 mm inner liner. Thirty-minute tows were made in depth strata less than 1000 m; tow time was one hour at deeper stations.

Initially, an equal number of tows was to have been made in each of four depth strata (75-150 m, 150-400 m, 400-1000 m, 1000-2000 m) in the canyon and slope areas. Variations in actual depth of tows, encounters with bottom types prohibitive to trawling and cruise time limitations combined to alter the program. The realized effort is presented in Table 1. Mean trawl depths were calculated from depths recorded at start and finish and at 3-minute intervals during each tow.

All red crabs were processed at sea. Carapace width (CW, distance between the tips of the lateral spines) and carapace length (CL, distance from the diastema between the rostral teeth to the posterior edge of the carapace, along the midline) were measured to the nearest millimeter. The latter measurement was emphasized based on recommendations of Gray⁴. Accuracy in weighing, which was done aboard ship, depended on sea state conditions. In most cases, weight was recorded to the nearest gram; some larger specimens were weighed to the nearest decigram.

Females were examined for evidence of egg extrusion and hatching. Color of eggs was noted for most females. External eggs from selected ovigerous females were examined microscopically to relate developmental stage to egg color. Developmental stages of ovaries of selected non-

⁴ Gray, G. W., Jr. 1969. Investigation of the basic life history of the red crab (*Geryon quinque-dens*). Rhode Island Div. Cons. Completion Rep. (P.L. 88-309, Proj. 3-46-R), pp. 36.

⁵ Ganz, A. R. and I. F. Hermann, 1975. Investigations into the southern New England red crab fishery. Rhode Island Dept Nat. Res. Div. Fish. Wildl. Mar. Fish. Sec. pp. 78.

⁶ Dias, C. A. and J. F. S. Machado. 1974. Preliminary report on the distribution and relative abundance of deep-sea red crab (*Geryon* sp.) off Angola, 8 p. In: Scientific papers presented to the second session of the International Commission for the Southeast Atlantic Fisheries (Madrid, December 1973), M. E. Bioceanol. Pescal. Angola, 12, pp. 75.

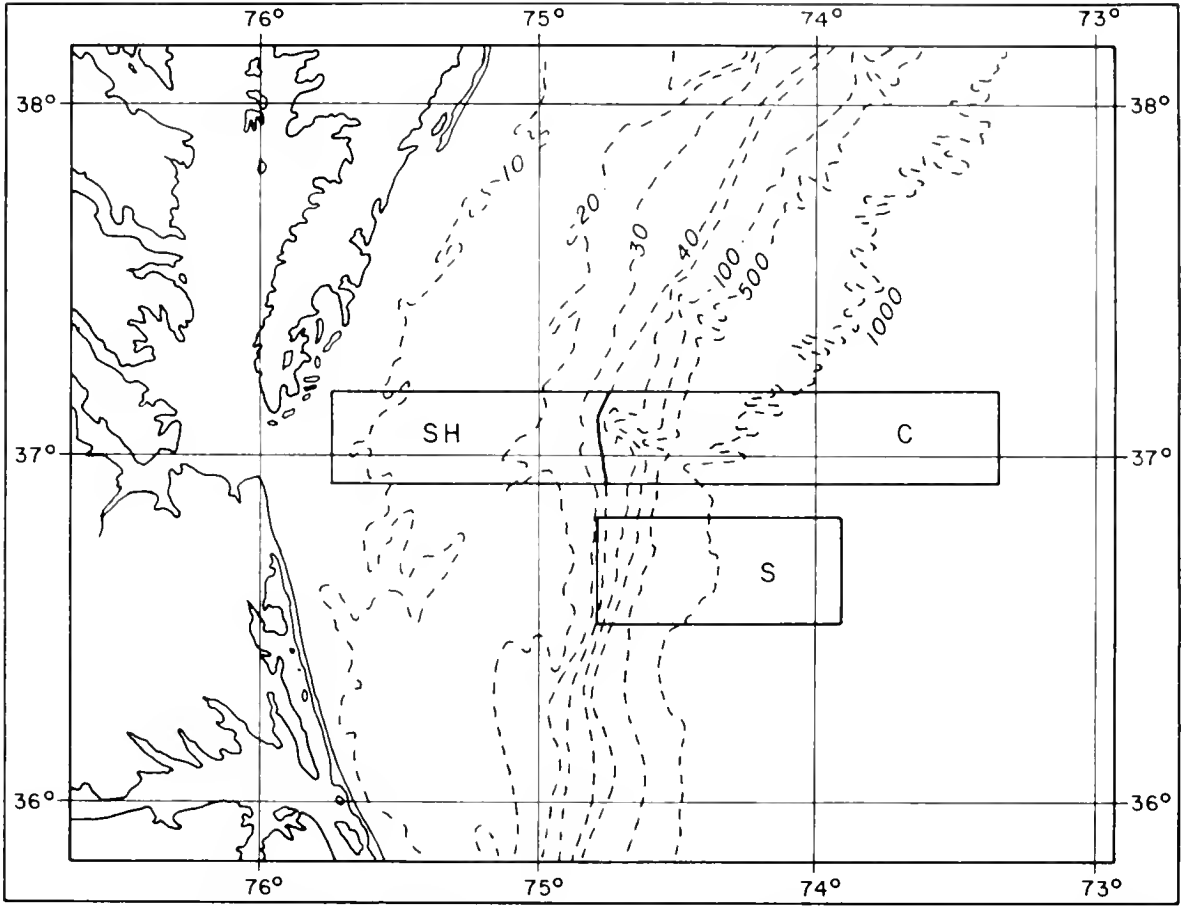


FIGURE 1. Chart of the Cheapeake Bight region of the western North Atlantic region showing shelf (SH), canyon (C) and open slope (S) trawl survey areas in the vicinity of the Norfolk Canyon. Isobaths in fathoms.

ovigerous females were classified as described in Haefner (1977).

Temperature and salinity of near-bottom water strata were monitored at trawl stations as well as at independent hydrographic stations. A variety of instruments was used including bathythermographs, expendable bathythermographs, a salinity-temperature depth recorder and reversing thermometers. Dissolved oxygen concentration of near-bottom water samples was determined by Winkler titration.

RESULTS AND DISCUSSION

Profiles of near-bottom (within 5-100 m of recorded depth) temperature and dissolved oxygen concentration (D.O.) for the four cruises are

presented in Figure 2. In all cases the data for canyon and slope areas are combined. The June plot reflects only data taken in conjunction with trawl stations; the other three plots include data from hydrographic and trawl stations. Only data from stations shallower than 1600 m are included.

Throughout the year temperature of near-bottom water was indirectly proportional to depth at depths exceeding 100 m (Figure 2). A large temperature gradient from 13°C to 6°C existed between 100 and 500 m. Below 500 m, temperature decreased gradually to 4°C at 1600 m.

Oxygen minima were associated with the thermal gradient (Figure 2). They were particularly obvious in June and November when D.O. values

TABLE 1. Norfolk Canyon demersal trawl fishing effort, expressed as number of tows, in the canyon (C) and on adjacent open slope (S) by season and by depth strata between 200 m and 1800 m.

Depth Stratum (m)	Spring		Summer		Fall		Winter	
	4-16 June 73		9-20 September 75		13-25 November 74		22-31 January 76	
	C	S	C	S	C	S	C	S
201- 300	6	1	3	1	1	2	2	2
301- 400	1	5	3	2	2	1	2	2
401- 500	1	0	0	0	0	0	1	1
501- 600	0	0	0	0	0	1	2	0
601- 700	1	1	2	2	3	3	0	1
701- 800	3	4	1	1	2	0	1	2
801- 900	0	0	2	1	0	1	1	1
901-1000	1	0	2	2	0	1	0	0
1001-1200	0	2	2	1	1	0	0	1
1201-1400	0	1	1	0	0	0	0	0
1401-1600	2	0	0	1	3	1	2	0
1601-1800	3	1	2	1	0	3	0	2
TOTAL	18	15	18	12	12	13	11	12

of 4.6 mg/liter were detected in near-bottom water within the 200-400 m depth range. Between 400 m and 800 m D.O. increased to 8 mg/liter, which persisted to a depth of 1600 m.

Except for shelf stations shallower than 200 m, salinity of near-bottom water was consistently between 35‰ and 36‰.

The 2539 red crabs caught during these cruises ranged from 16 mm to 143 mm in carapace length (CL). For purposes of comparing carapace length with carapace width (CW) reported in other papers, the following relationships were derived for 308 males, CL range 18-138 mm:

$$CW = 8.74 + 1.09 CL, r = 0.98$$

and for the 269 females, CL range 23-116 mm:

$$CW = 11.04 + 1.06 CL, r = 0.98$$

Male crabs attain a larger size than females. The largest male crab caught measured 143 mm CL and weighed 1200 g; the largest female was 123 mm CL and weighed 510 g. The following wet weight-length relationships were derived for 238 males ranging from 3 g to 1200 g:

$$\log \text{ male weight} = -3.58 + 3.14 \log CL,$$

$r = 0.99$ and for 142 females ranging from 4 g to 510 g:

$$\log \text{ female weight} = -3.13 + 2.88 \log CL,$$

$r = 0.97$.

Although the size frequency distributions (Figure 3) indicate that the red crab is obviously not vulnerable to the trawl gear, certain modal groups (CL) were recognized in nearly every season. The most obvious were the 90-130 mm group for males and the 75-110 mm group for females. Other modal groups, such as 50-90 mm for males and 50-75 mm for females were less obvious. Wigley, Theroux and Murray (1975), in a survey extending from offshore Maryland north-eastward to Corsair Canyon on Georges Bank, observed similar modal groups for male crabs. Their female size frequency curve, however, did not indicate a well-defined intermediate group. On the other hand, their well-defined peak for red crabs less than 30 mm CL was missing from Norfolk Canyon samples.

Analysis of the Norfolk Canyon data using a three-point moving average, with subsequent calculation and plotting of percent cumulative frequency on probability paper was encouraging. Thirteen to fifteen smaller, less pronounced modes were detected which suggest molt classes within the larger modal groups. If, indeed, the smaller modes were representative of molt classes, a 6 to 11 percent range in growth increment (CL) is suggested. This range is comparable to four of the five

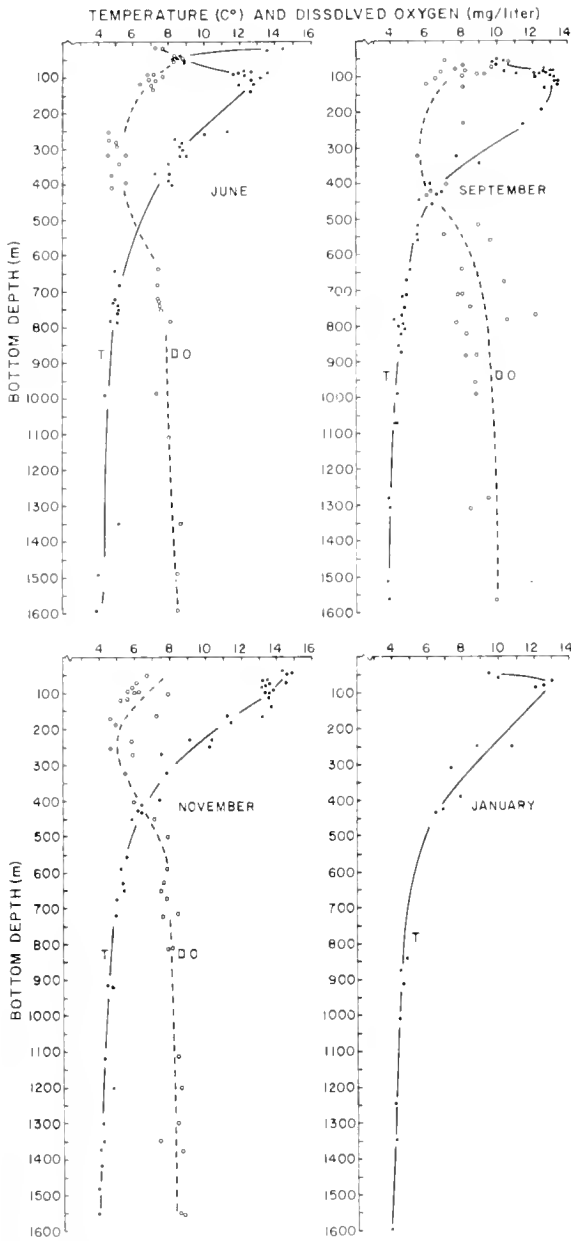


FIGURE 2. Seasonal profiles of temperature (T) and dissolved oxygen (D.O.) of near-bottom water in relation to depth in the Norfolk Canyon and adjacent shelf and slope area.

observations (6.7, 8.5, 8.9, 10.4, 18.1%) of Gray⁴ of crabs molting in the laboratory. One red crab molting at VIMS increased in length by 13.8%.

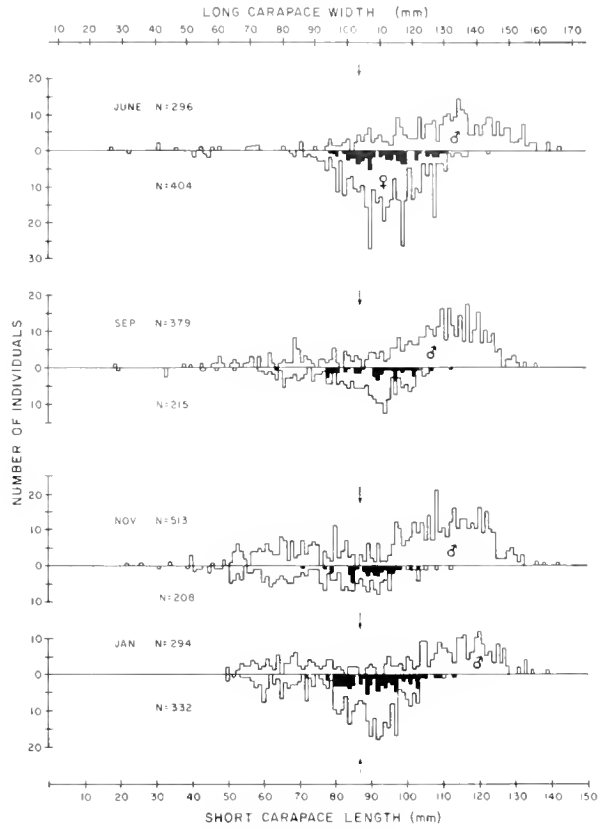


FIGURE 3. Seasonal size frequency distributions of *Geryon quinquedens*. Males are plotted above the line; females below. Black areas indicate ovigerous individuals and those with egg remnants on the pleopods.

Vertical arrows indicate present acceptable market size. Scales for carapace length and carapace width are included for comparative purposes.

Crabs less than 70 mm CL were poorly represented in the June sample (3% of the catch), but they made up an increasingly larger proportion of the catch through September (13.8%) and November (22.9%). The proportion in January (16.4%) was largely due to the absence of crabs less than 50 mm CL.

Over 50% of all Norfolk Canyon red crabs were larger than 96 CL (114 mm CW), the minimum size presently acceptable to processing plants (Wigley, Theroux and Murray, 1975). This proportion varied by sex, season and depth (Table 2).

Table 2. Number of *Geryon quinquedens* caught and percentage exceeding carapace length of 96 mm, arranged by depth and by season.

Depth (m)	JUNE				SEPTEMBER				NOVEMBER				JANUARY				TOTAL				
	Male		Female		Male		Female		Male		Female		Male		Female		Male		Female		
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
201-300	0		0		8	62.5	65	27.7	1	0	0	0	0	0	0	0	0	9	55.6	65	27.7
301-400	115	94.7	288	44.4	21	90.5	59	33.8	13	92.3	23	26.1	19	84.2	13	53.8	108	92.9	383	42.0	
401-500	12	100.0	32	75.0	0		0		0		0		72	84.7	182	19.2	84	86.9	214	27.5	
501-600	0		0		0		0		31	90.3	17	11.8	35	65.7	87	22.9	66	77.3	104	21.2	
601-700	36	72.2	7	14.3	136	63.9	32	9.1	228	72.3	87	5.7	21	61.9	4	50.0	421	69.1	130	8.5	
701-800	117	67.5	84	11.9	14	71.4	4	0	165	40.6	54	1.9	54	84.9	8		350	57.7	150	7.3	
801-900	0		0		44	90.9	10	10.0	17	64.7	3	0	86	32.6	39	0	147	53.7	52	1.9	
901-1000	18	72.2	1	0	105	79.0	20	5.0	34	88.2	10	10.0	0		0		157	80.3	31	6.5	
1001-1200	0		0		35	62.9	8	0	5	100.0	0		7	85.7	1	0	47	70.2	9	0	
1201-1400	0		0		15	80.0	16	0	0		0		0		0		15	80.0	16	0	
1401-1600	0		1	0	0		0		19	63.2	11	0	0		0		19	63.2	12	0	
1601-1800	0		0		1	0	0		0		0		0		0		1	0	0		
TOTAL	296	80.7	414	39.4	370	73.4	214	20.1	513	64.3	203	7.4	294	65.6	334	19.2	1482	70.2	1165	24.5	

Potentially marketable male crabs constituted 70% of total males caught whereas less than 25% of the females exceeded 96 mm CL, a reflection of the larger ultimate size of male crabs. Seasonally, the proportions were consistent for males, but varied for females. A high proportion of females (39%) in June reflected the absence of small modal groups at that time; a low of 7.4% in November was related to a reduced modal group of large females.

These figures are markedly higher than the percentage (24%) of harvestable crabs in the northeast red crab survey (Wigley, Theroux and Murray, 1975). However, any comparisons between the two geographic areas must be qualified. Differences in size frequency distributions of the two populations are most likely related to the differences in sampling methods.

Comparison with other geographic regions is further complicated by difference in the acceptable harvestable size as well as in method of catch. For example, the minimum size of red crabs for the Ivory Coast of Africa is 84 mm CL (100 mmCW) (Intes and LeLeouff, 1976). In their survey 70% of the total catch of red crabs (38% of all males) was legal. If 84 mm CL instead of 96 mm CL was the accepted minimum market size in the United States, the percentage of potentially marketable male crabs caught in the Norfolk Canyon survey would increase from 70% to 78% and the percentage of marketable females would increase from 50% to 65%.

The proportion of large males in the population was consistent over most of the depth range (Table 2). Most of the larger females were found in relatively shallow water, <600 m.

The inverse relationship between water depth and crab size observed by Wigley, Theroux and Murray (1975) was also evident for females from 200 m to 1500 m and for males only in the 200-500 m depth range in the Norfolk Canyon region (Figure 4). The mean size of male crabs caught deeper than 600 m was fairly constant. Apparent seasonal variations shown in Figure 4 are due to lack of samples (Table 1) and/or low number of specimens in certain depth strata.

Red crabs were contagiously distributed within the Norfolk Canyon survey area within the total depth range of capture (220-1800 m), as well as within the 300-1000 m range of most consistent

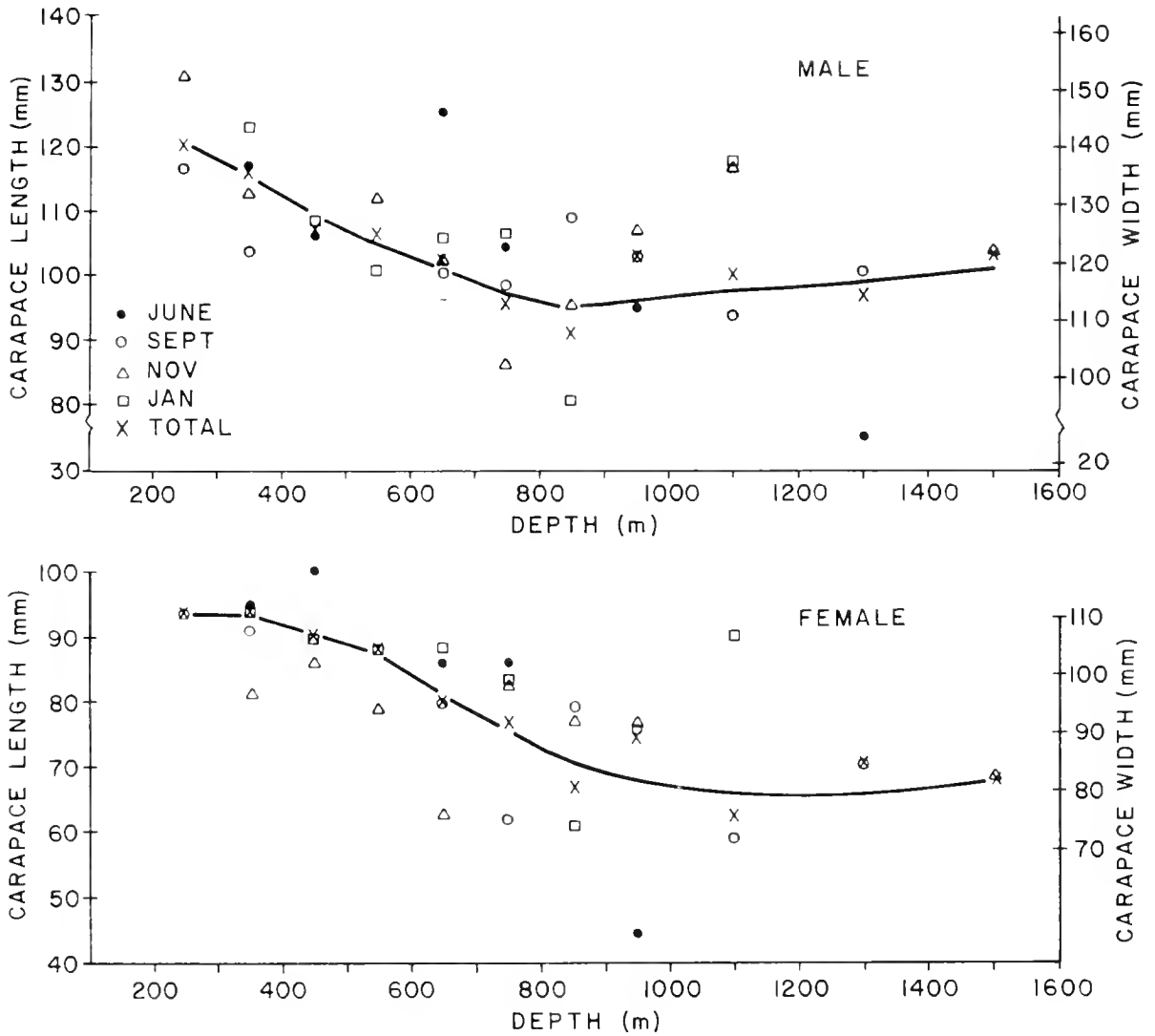


FIGURE 4. *Geryon quinquedens*. Relation of mean size of males and females to depth according to season and for all seasons combined. Scales for carapace length and width are included for comparative purposes.

catches. Because there was an excess of samples with zero catch and the variance exceeded the mean number of crabs per tow ($\bar{X} = 23.3$ within 200-1800 m; $\bar{X} = 39.5$ within 300-1000 m), catch data were transformed (Elliott, 1971) as an index of abundance: $Y = \frac{1n}{n(x+1)}$ where x is the number of red crabs caught per 30 minute tow in any given stratum and n is the number of tows at any given depth. Data from the hour long tows were adjusted to correspond to half hour tows.

Red crabs were significantly ($P = 0.001$) more abundant on the adjacent slope than in Norfolk Canyon proper (Figure 5). Although stratifying depth by 100 m and 200 m intervals emphasizes voids in actual sampling depth (Table 1), it is evident that the distributional depth range is broad, from 200 to 1800 m (actual fishing depth range was 210 m to 1725 m). Most hauls were successful in catching crabs within the 400-1000 m zone (actual fishing depth 405 m to 1042 m) where relative

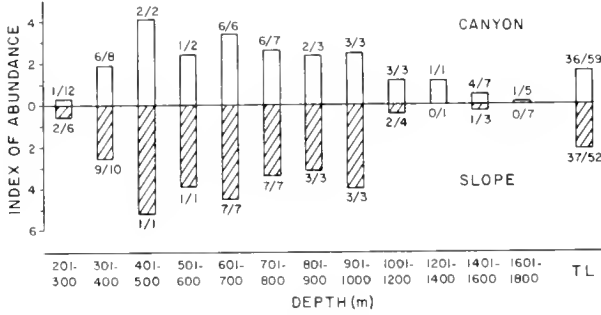


FIGURE 5. Relative abundance of *Geryon quinquedens* by area, expressed as index of transformed mean number of crabs per half-hour tow within each depth stratum. Fraction above or below each bar is the ratio of the number of stations at which red crabs were captured to the total number of stations in each stratum.

abundance was highest. The actual distributional depth range is most likely 210-1565 m because the single individual recorded for the 1601-1800 m stratum is suspected to be a wash-down from a previous sample.

In light of the temperature-dissolved oxygen-depth relationship, it is clear that the majority of the red crab population inhabits bottom waters deeper than 400 m which are overlain by cold, well-oxygenated water (Figures 2,5). A smaller percentage of tows caught crabs in the shallower (<400 m) areas where warmer, oxygen minimum water existed.

Females were more abundant than males in samples from depths shallower than 600 m; males dominated the catches in deeper water (Figures 6,7H). This segregation of the sexes by depth has

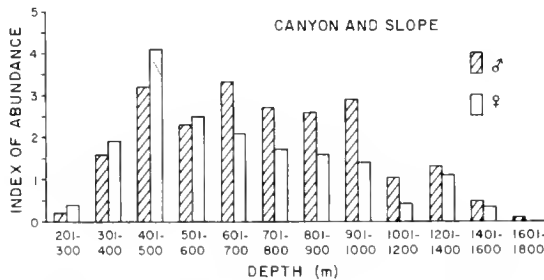


FIGURE 6. Relative abundance of *Geryon quinquedens* by sex, expressed as index of transformed mean number of crabs per half-hour tow within each depth stratum.

been observed in other areas. In Rhode Island waters Ganz and Herrman (1975) observed a lack of females between 700 m and 915 m; the greatest percentage of males was caught in 685-1110 m. The survey of Wigley, Theroux and Murray (1975) indicated a marked reduction of the number of females in water deeper than 500 m, where males predominated. Basically the same pattern was observed off the coasts of Angola

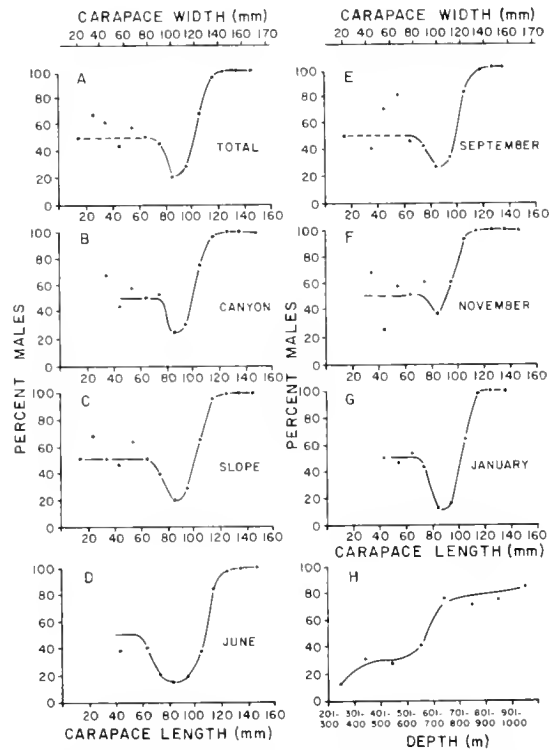


FIGURE 7. Percentage of Male *Geryon quinquedens* by size and depth. Data expressed as probability curves for total catch, area, season and depth. Scales for carapace length and width are included for comparative purposes.

(Dias and Machado^o) and Abidjan (Ivory Coast) (LeLoeuff, Intes and LeGuen, 1974; Intes and LeLoeuff, 1976); the largest male catch was recorded from 600-700m; females were largely restricted to 300-400 m. A 400-600 m zone of transition was recognized wherein males and females occurred in variable, but nearly equal numbers.

The combined, four-cruise male: female ratio was 1.28:1, significantly different from the

theoretical 1:1 (Chi-Square, $P = 0.01$). The ratio varied from cruise to cruise with significant differences (M:F) in September (1.77:1), November 2.51:1 and June (0.73:1). The 0.88:1 ratio in January was not significant.

The presentation of sex ratio data in the form of probability curves (Wenner, 1972) is more meaningful. Red crab data were tabulated into 10 mm size classes and the sex ratio (as percent males) calculated within each class and plotted. The "anomalous" pattern shown for total red crab catch (Figure 7A) is not appreciably different than that for location (Figure 7B, C) or season (Figure 7D-G). Scatter about the curves is due to low numbers of individuals in the smaller size classes. The "anomalous" pattern is consistent with the Fisher theory (Wenner, 1972) in which a 1:1 offspring production is favored by natural selection, but a unique deviation from the 1:1 ratio is illustrated for older or larger animals.

The observed pattern is principally a function of physical size. The shape of the curve for red crabs exceeding 100 mm CL is determined by the larger maximum size of male crabs. Although growth rate and longevity are presently unknown for *Geryon*, it is known that females reach maturity at 65-75 mm CL, (Haefner, 1977) and continue to molt to eventually attain at least 116 mm CL. Males most likely reach maturity near 65-75 mm CL but attain a larger maximum size than females, either by more frequent molts, larger molt increments, living longer or by a combination thereof.

The paucity of males and an accumulation of females distributed about 85 mm CL (Figure 3) shows up as a dip in the probability curve. The accumulation of females in the large modal size group bracketing 85 mm CL could be due to longer intermolt intervals, smaller growth increments, terminal anecdyosis or inhibition of molting by vitellogenesis and spawning (oviposition). Such inhibition is known to occur in other crustaceans (Adiyodi and Adiyodi, 1970; Swartz, 1976).

The study of the reproductive biology of females was based on individuals exceeding 70 mm CL (85 mm CW), which includes most of the mature females (Haefner, 1977). This manipulation insures that most of the reproductively

mature segment of the female population is treated and reduces data bias due to variations in catch of smaller size classes. (Figure 3).

Wigley, Theroux and Murray (1976) related color of the external egg to developmental stage. Within the red-orange, brown, dark brown, purple and black spectrum, they judged newly deposited eggs to be light red or orange; eggs become darker as they ripen.

A microscopic examination of eggs from 11 extruded egg masses (sponges) from Norfolk Canyon crabs indicated a large variation in color within the earlier stages of development (Table 3). Because of the obvious difficulty in assigning specific development stage by color alone, the observed colors were grouped into early (A-C; orange-brown) and late (D; burgundy-purple-black) categories according to the scheme in Meredith (1952).

A spawning cycle is suggested for red crabs in the Norfolk Canyon area although ovigerous females were captured in all seasons (Figure 8).

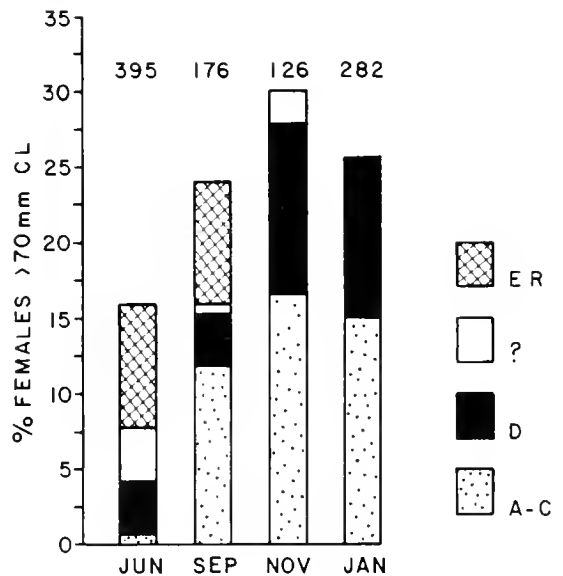


FIGURE 8. Seasonal percentage of early (A-C) and late (D) developmental stages of extruded eggs on ovigerous individuals and of egg remnants (ER) on total catch of female *Geryon quinqueedens* >70 mm CL captured in the vicinity of Norfolk Canyon. Blank areas indicate unidentified egg stage. Sample size indicated by numbers above the bars. Egg stages are described in Table 3.

TABLE 3. *Developmental stages of external eggs of Geryon quinque-dens. Size range based on measurements of 10 eggs from each sponge. Modified from Meredith (1952).*

Stage	Number of Sponges Examined	Description	Size Range (μm)	Color
B	7	Egg early to late blastoderm; nearly spherical. Minute eyes visible in larger embryos.	640-740	Orange Red-orange
C	2	Eye $\frac{1}{3}$ - $\frac{1}{2}$ size of Stage D embryo; eye the only pigmented (brown) area. Yolk abundant. Abdomen free. Abdomen without melanophores.	710-780	Red-brown Orange Red-orange
D	2	Pre-larval embryo. Eyes large. Abdomen and appendages well-developed, free from head. Red-brown pigmentation present, light over entire body, intense in eyes, cardiac and gastric regions of carapace, and in dorsal abdominal melanophores.	720-820	Burgundy Purple (black)

The presence of females bearing egg remnants and the low incidence of ovigerous individuals in June suggests a high incidence of egg hatching between January and June. This is based on the assumption that the presence of egg remnants indicates recent spawning. However, at the present time it is not known how long egg remnants remain on the pleopods. Hatching continues through the summer and is accompanied by an increase of ovigerous females bearing early stage (A-C) eggs. The peak incidence of ovigerous females occurs in November. This is characterized by a high percentage of females with late stage (D) eggs and a peak incidence of recently extruded (A-C) eggs. The percentage of ovigerous females in the population remains high in January, and although it is somewhat less than that observed in November, it is similar in the proportional makeup of early and late stage eggs.

Information on incidence and relative abundance of red crab larvae in plankton samples would help to resolve the presence or absence of a spawning cycle, but such data are presently unavailable or incomplete. Winter and spring samples off the coast of New Jersey have revealed very few first and second zoeal stages (P.O. Smyth, VIMS, personal communication). This indicates some hatching has occurred in winter and spring. Analyses of summer and fall samples are incomplete.

The ovarian cycles of non-ovigerous females (Figure 9) complements the spawning pattern. From June to September, there was no major change in ovarian stage. In November, an increase in the incidence of developing (intermediate) ovaries was accompanied by a decrease in advanc-

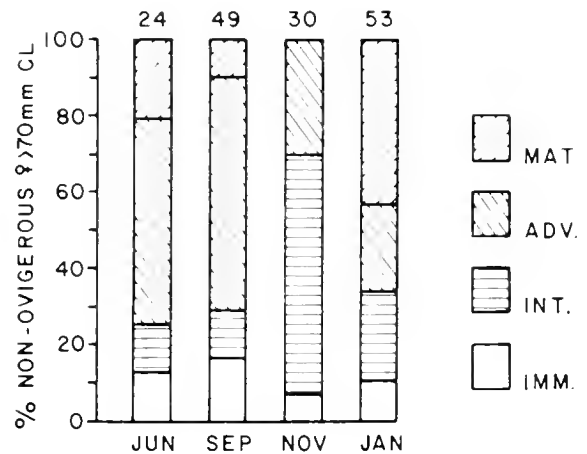


FIGURE 9. *Seasonal proportion of ovarian developmental stages (MAT, mature; ADV, advanced; INT, intermediate; IMM, immature) among samples of non-ovigerous female Geryon quinque-dens >70 mm CL captured in the vicinity of Norfolk Canyon. Sample size indicated by numbers above the bars.*

ed/mature ovaries. The lack of mature (ripe) ovaries in November complements the peak incidence of ovigerous females at that time, suggesting that most of the mature females have extruded their eggs. Continued progressive development results in the higher proportion of advanced and mature gonads observed in January.

The temperature regime appears to determine the distribution of ovigerous females, the majority of which were captured in 400-800 m depths where temperatures exceeded 5° C (Figure 2.) Ovigerous females were captured over an extensive depth range in Norfolk Canyon although the evidence shown for the 1201-1400 m stratum is due to only two individuals in a small sample (Figure 10). The highest incidence of occurrence clearly fell within the 401-800 m depth range. Females with external eggs in early stages of development were found deeper than 300 m and were most frequently found within the 401-700 m depth range. The late

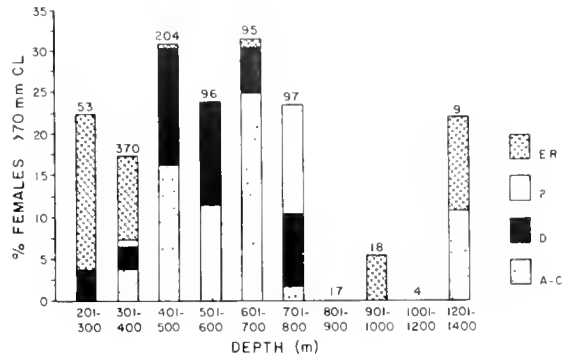


FIGURE 10. Depth distribution of ovigerous red crabs by egg development stage (A-C, D) and of females with egg remnants (ER) on pleopods, expressed as percentage of total catch of females >70 mm CL. Blank areas indicate unidentified egg stage. Numbers above the bars indicate number of females in sample. Egg stages are described in Table 3.

TABLE 4. Density of red crabs (no./hectare) captured by 13.7 m trawl and standing crop (in thousands of crabs) in vicinity of Norfolk Canyon (36°30' —37°10' N).

Depth (m)	September 1975		January 1976		All	
	No./ha	Crop 1000's	No./ha	Crop 1000's	No./ha	Crop 1000's
200-300	8.5	67.0	0	0	4.3	33.9
300-400	31.1	199.2	5.6	35.9	14.5	92.9
400-500	—	—	60.7	35.6	60.7	35.6
500-600	—	—	125.4	793.8	125.4	793.8
600-800	18.1	210.0	16.3	189.2	17.5	203.1
800-1000	23.6	337.3	51.4	734.5	30.4	434.4
1000-1200	8.6	162.5	14.4	272.1	9.2	173.8
1200-1400	31.9	703.7	—	—	31.9	703.7
1400-1600	0	0	0	0	0	0
1600-1800	0.1	4.9	0	0	0.1	4.9
All	13.2	2599.1	19.6	3859.3	15.8	3111.1

stage of development was most abundant at 401-800 m depth, but it was the only stage present in the 201-300 m depth stratum. Females with egg remnants were caught within an extensive depth range but were markedly more prevalent in shallower water (201-400 m) than in any other depth.

These data do, to a certain extent, corroborate the findings of Wigley, Theroux and Murray (1975) of an increase of spawning females with depth (to 640 m for their northeast sample), but there is no evidence from the Norfolk Canyon data to indicate seasonal differences in the incidence of early and late stage eggs with depth.

The presence of stage D eggs at 201-300 m (Figure 10) is due to September collections only and the high incidence at 701-800 m is due primarily to June collections. Only the females with egg remnants are restricted to two seasons, but the data for June and September (Figures 8, 9) are consistent with that shown in Figure 10. This preponderance of females with egg remnants in water warmer than 8° C (in June, they were captured in 300-400 m depth stratum) may not be coincidence. The migration of ovigerous females, with eggs in advanced stages (D) of development, into shallower, warmer water may enhance egg development and hatching. Although mortality of eggs and larval development as a function of temperature has not been determined, it is known that eggs survive and hatch at 15° C and larval development proceeds at temperatures as warm as 21° C (Perkins, 1973).

Relative density of red crabs was estimated for the September 1975 and January 1976 surveys (Table 4) when tow distances could be determined with reasonable accuracy from Loran C readings. Area fished was then computed from tow distance and the effective fishing width of the net, estimated to be 7.6 m (Haedrich, Rowe and Polloni, 1975). This accounted for 55.4% of headrope length, a value near the lower end of the range of values computed for other types of trawls (Griswold, Kurlyandsky and Twohig, 1971).

The relative densities were then used to compute standing crop estimates for the immediate fishing zone (Table 4). Area of each depth stratum within the zone was determined with a planimeter using a base chart constructed by E.P. Ruzicki (VIMS).

The relative densities of red crabs in the area of Norfolk Canyon were 50-95% lower than those observed for more northeasterly areas of the continental shelf and slope (Grassle et al., 1975; Wigley, Theroux and Murray, 1975) although a fair degree of overlap exists within the range of values of these three studies.

The low red crab density in the Norfolk Canyon area is most likely a reflection of the inefficiency of the collecting gear. The ineffectiveness of trawl nets in capturing contagiously distributed, motile megabenthic invertebrates has been revealed in certain gear comparison studies (R. Cooper and J. Uzmann, NMFS, personal communication). Ad-

mittedly, crab density calculations based on trawl catches are tenuous because of a number of variables (Wigley, Theroux and Murray, 1975). However, in order to compare their data with mine, I converted their trawl catches to relative densities (Table 5) and found that they fell short of the values determined by photographic sled. Their trawl densities, ranging from 19% to 78% of the

TABLE 5. Comparison of red crab densities determined by photographic sled and those computed for 4.9 m trawl for total geographic zone. Data source: Wigley, Theroux and Murray (1975).

Depth (m)	Red Crab Density		Percent of Sled Density
	Sled	Trawl	
229-320	21.1	16.5	78.4
320-412	258.3	190.2	73.7
412-503	273.2	136.5	50.0
503-640	282.0	53.8	19.1
640-914	91.4	45.5	49.8
914-1280	61.0	37.2	61.0
1280-1646	10.9	0	—

photographically estimated densities, were computed from an assumed vessel speed of 1.75 knots for a duration of 30 minutes, and an effective fishing width of 3 m for the 4.9 m (16 ft) trawl (Haedrich, Rowe and Polloni, 1975).

The small trawl is apparently more effective in capturing red crabs than is the large trawl. Although the larger net sweeps more than twice the area of bottom in a given unit of time, it is unable to capture twice the number of crabs, assuming the same density of crabs is available (vulnerable) to the gear. Although it is difficult to accept the apparent superiority of the 4.9 m trawl over the 13.7 m trawl in capturing red crabs (compare Tables 4 and 5), the fact is that it yielded larger catches on an equal effort basis (0-218, \bar{x} = 33; 0-197, \bar{x} = 23 crabs/30 minute tow, for small and large trawl, respectively). The relative ineffectiveness of the large net may be due to a number of factors such as lift of the net from the bottom and rolling over crabs in depressions. Net avoidance, however, is not likely a factor; a small net could be more easily avoided than a larger net.

There remains the possibility that the red crab stock in the Norfolk Canyon area may be relatively sparse compared with stocks distributed north-

easterly along the shelf and slope. This dilemma will not be resolved until the stocks are more effectively evaluated by tagging, gear comparison and calibration.

Other studies either cannot be compared to ours or to that of Wigley, Theroux and Murray (1975) because of variation in gear used (Schroeder, 1955, 1959). Furthermore, they present conflicting values. For example, Grassle et al (1975) determined red crab densities using photographic techniques in DSRV *Alvin*. Their values from two dives (180 crabs/ha in 495-499 m depth; 19.4 crabs/ha in 992-1000 m) represented 64% and 22%, respectively, of the photographic sled densities reported by Wigley, Theroux and Murray (1975) within the same geographic zone.

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**FISHERY BIOLOGY OF SPINY LOBSTER
(*PANULIRUS ARGUS*) of the GUAJIRA PENINSULA OF
COLOMBIA, SOUTH AMERICA, 1969-1970**

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UNDP/FAO PROYECTO PARA EL DESARROLLO
DE LA PESCA MARITIMA EN COLOMBIA, BOGOTA, D.E.

ABSTRACT

The fishery for *Panulirus argus* of the Guajira Peninsula of Colombia is reported to average 550 tons (total weight) a year since 1969. However, an annual catch of 20 tons from traps in an estimated area of 40 km² in 1971 is evidence of a potential yield of 1,000 tons annually from the total area of about 2,000 km² of smooth bottom where turtle grass and coralline outcroppings occur in depths of 5-50 m. Spawning (and possibly molting) in almost all mature females was estimated to occur every two months. With molt increments of about 6mm cl, hypothetical gains from original weight on molting are approximately 35% for one, 70% for two, 100% for three and 150% for four molts on the average. The period of oogenesis (development of ova in ovaries) is about equal to embryogenesis (development of embryos in eggs on pleopods) and most females are ready to spawn again when eggs are hatched. About 300,000 eggs are carried at 75 mm cl and 1 million at 110 mm cl. Females carry eggs as early as 64 mm cl but about 50 % were immature at 71 mm cl. A minimum size of 76 mm cl (at least) is recommended for this area where smaller ones are sometimes exploited.

INTRODUCTION

Spiny lobsters (*Panulirus argus* and *P. laeviscauda*) are found all along the coast of the Guajira Peninsula, the eastern part of the Colombian coast adjacent to Venezuela (Figure 1). A commercial fishery for lobsters occurs west of Cabo de la Vela where there is a shelf gradually sloping to the 50 m contour and averaging 20 km in width. Where lobsters are found is estimated to be 130 km long and 15 km wide, an area approximately 2,000 km². All this area is not necessarily fished by the Guajiros, a tribe of Arawak Amerindians who dive reportedly to about 10 m deep (us-

ing face masks only), nor by other coastal fishermen who use Florida-type wooden traps in depths of 10-25 m. The landings reported since 1969 (Table 1) average about 550 tons (live weight) a year, a small but significant amount when compared with the total annual Caribbean catch of 13,000 tons (Gulland, 1970). The fishery provides an important cash income for the coastal peoples of the Guajira.

The coastlands of the Guajira Peninsula are low-lying and semi-desert with several large lagoons, some of which are used for solar salt production and have rocky or sandy substrate, while others are fringed at least partly by mangroves and have mud substrate. Just offshore throughout the area are extensive beds of turtle grass (*Thalassia testudinum*) interspersed with smooth sandy bottom and outcroppings of coralline rock

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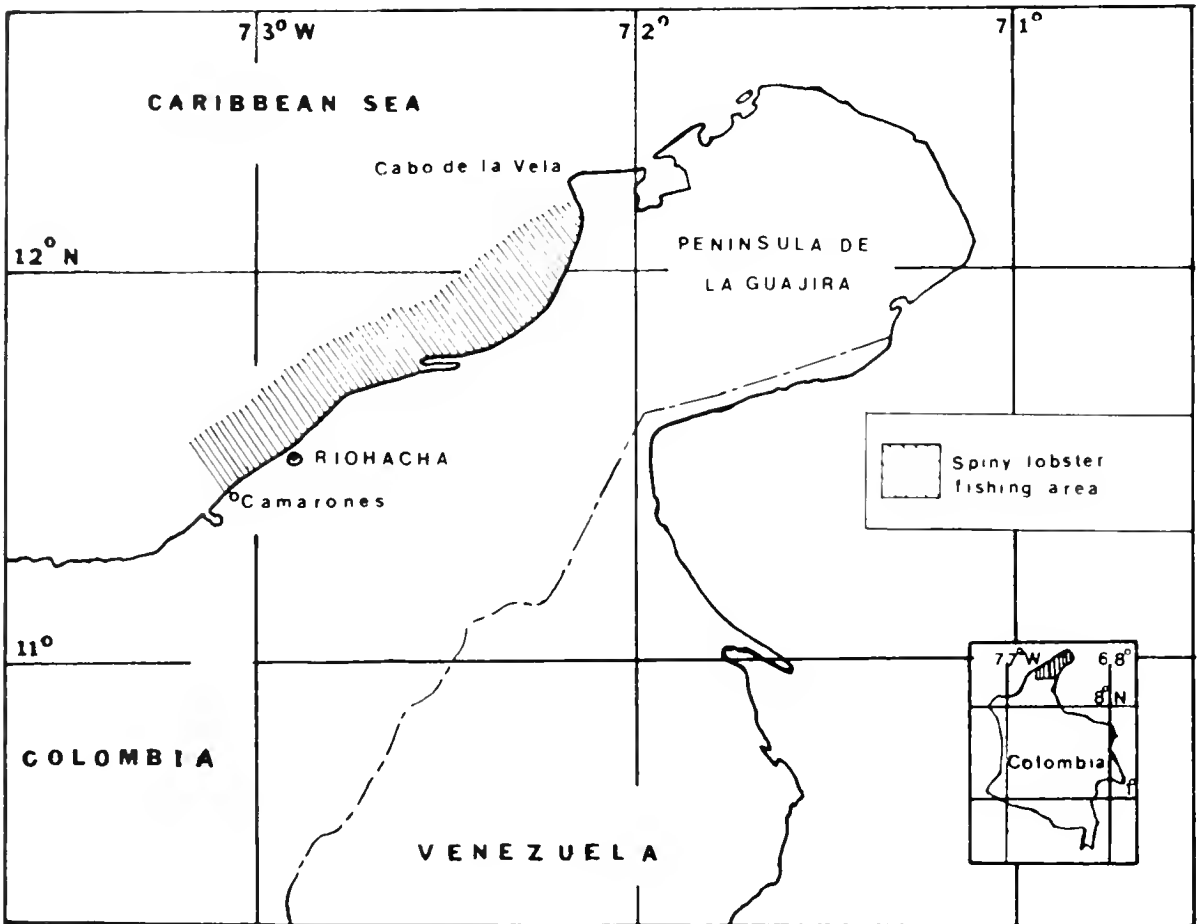


FIGURE 1. Map of the Guajira Peninsula of Colombia showing fishing grounds for spiny lobsters, *Panulirus argus* and *P. laevicauda*, and place names used in the text.

or fossil oyster reef. Immediately west of Cabo de la Vela is an indentation of the coast (Figure 1) where large numbers of small lobsters are reported throughout the year, and it is possible that current patterns encourage settlement of lobster larvae from the plankton. Navigation charts show currents of up to 1.2 knots setting westward off Cabo de la Vela. These would be under the influence of northeast and easterly trade winds in the area. Also near the coast are weak counter currents (0.9 knots) setting eastward along the shore of the Guajira Peninsula. It is likely, therefore, that a weak anti-cyclonal gyre is set up just west of Cabo de la Vela.

The present study of the spiny lobsters in this area was undertaken to make an estimate of their

potential yield to a fishery and to determine some essential features of their biology such as reproduction, growth and feeding habits.

TABLE 1. Annual catches of *Panulirus argus* from the Guajira Peninsula of Colombia, 1969-74.

Year	Total weight tons
1969	800
1970	870
1971	540
1972	300
1973	270
1974	420

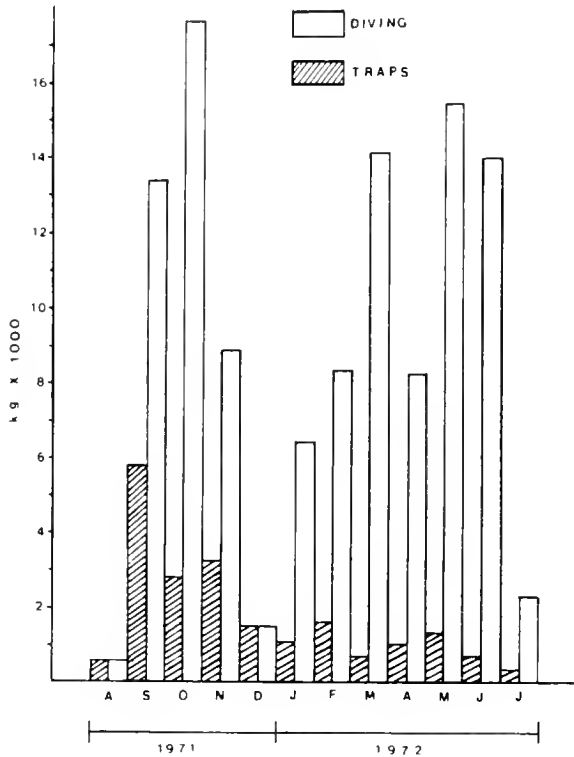


FIGURE 2. Histogram of monthly catches of *Panulirus argus* handled by a processing company, including those caught by Florida-type wooden traps and diving near Riohacha, Guajira Peninsula of Colombia, 1971-72.

METHODS

Monthly trips were made to Riohacha (Figure 1) where freezing and cold storage facilities were located and the spiny lobster catch being processed for export (total cold storage was about 20 tons and freezing capacity about 3 tons daily in 1970). Data on catch were supplied by the processing company and INDERENA (Instituto de Desarrollo de los Recursos Naturales Renovables).

Measurements and examinations of the spiny lobsters were made from random samples of live catches brought to the company for processing. Samples were taken by setting aside all specimens from a segment of a heap of lobsters emptied from burlap bags on the concrete floor of the processing room. Each lobster in the samples was measured and examined as follows:

Lengths and weights to the nearest mm or g.

Each lobster was weighed whole (TW) on a commercial balance (accurate to about 5 g);

carapace length (CL) from the anterior edge of the carapace between the two large supraorbital spines to the posterior edge in the mid-dorsal line with vernier calipers; total length (TL) on a measuring board (stretched with back against the board) with the supraorbital spines against the headboard (3 cm high) and the length read where the tip of the telson reached on the board; the abdomen (tail) was then separated from the thorax (head) and weighed on the balance (AW), then stretched on the measuring board back down with the anterior edge of the first segment pressed against the headboard and the length (AL) read where the tip of the telson reached on the board; the greatest width of the abdomen (at the second segment) was taken on the measuring board by pressing the ventral edge of the pleuron of one side against the headboard and reading the width where the edge of the pleuron of the other side reached on the board.

Examination for maturity, etc.

Ovaries were removed from the thorax and their colour recorded. Greater diameter of a few ova from part of the ovary was measured under magnification (10X) on a transparent mm grid. When eggs were carried on the pleopods they were removed before weighing the abdomen. The color of the egg mass was recorded and the phase of embryo development noted under magnification (10X). Hardness or newness of the shell, presence of epifaunal growths, etc., were also recorded (New shell was defined as recently molted but sufficiently rigid to permit capture and handling. It was bright in color and free from epifauna or discoloration and buckled under light pressure). Stomachs seen to contain food were taken out and preserved in formalin for later examination.

Temperatures and salinities were taken with a portable salinometer from a beach site, from the head of the jetty at Riohacha and from lobster fishing stations by the R/V CHOCO (March 9-16, 1970).

Landings from lobster traps and from diving for one year were provided by one of the lobster processing companies at Riohacha.

BIOLOGY

Length-weight relationships.

Regression equations for total length at each carapace length in males and females were as follows:

Male $TL = 2.34 CL + 39.4$ ($N = 500$);

Female $TL = 2.40 CL + 47.9$ ($N = 493$).

The rate of increase in total length relative to carapace length appeared to be greater in females than in males over the range of commercial sizes (Figure 3). However, in spite of the large numbers used an appreciable overlap in the regression coefficients is apparent in a "t" test (Spiegel, 1960) showing a range of 2.24 - 2.44 in males and 2.29 - 2.51 in females so that both could be similar (Table 2).

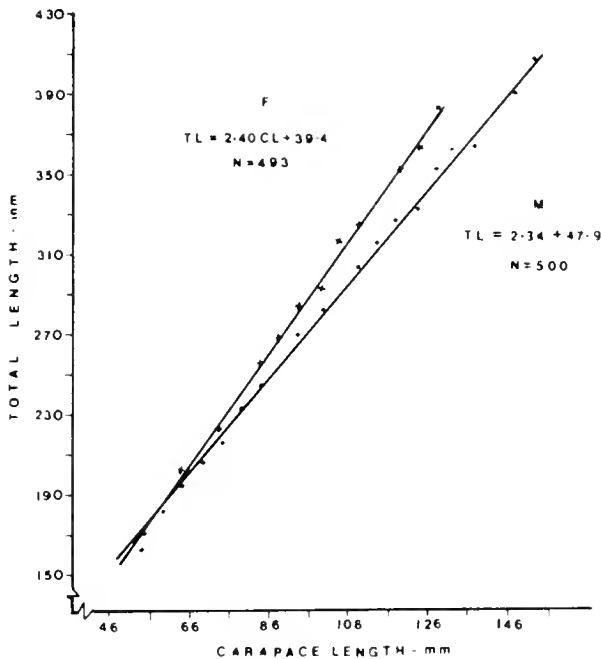


FIGURE 3. Regression of Total Length (TL) on Carapace Length (CL) in male and female *Panulirus argus* from the Guajira Peninsula of Colombia.

Regression equations for abdomen length relative to carapace length give divergent slopes as follows (Figure 4):

Male $AL = 1.34 CL + 32.1$ ($N = 500$);

Female $AL = 1.56 CL + 17.1$ ($N = 493$).

The slope for females is the steeper indicating that the increase in length of abdomen relative to carapace length is greater in females than in males. The ranges in coefficients shown by a "t" test support this, being 1.27 - 1.41 in males and 1.51 - 1.61 in females (Table 2).

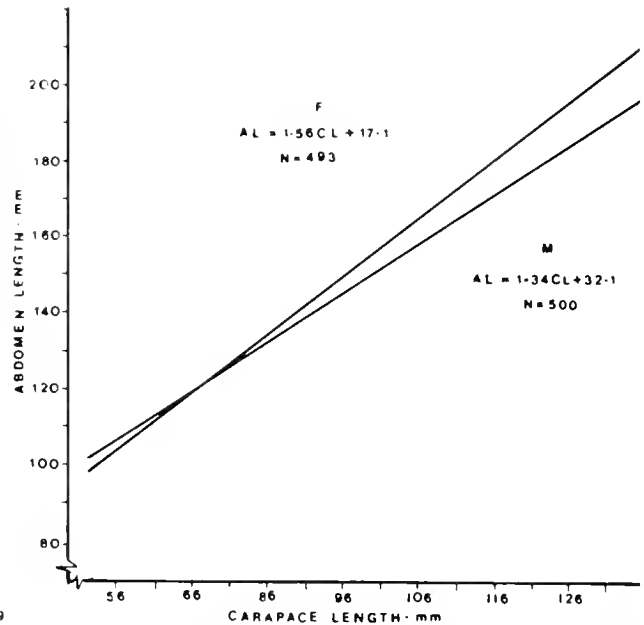


FIGURE 4. Regression of Abdomen Length (AL) on Carapace Length (CL) in male and female *Panulirus argus* from the Guajira Peninsula of Colombia.

TABLE 2. Regression equations and "t" test of regression coefficients of length and weight relationships of *Panulirus argus* from the Guajira Peninsula of Colombia. Calculation of "t" test from Spiegel (1961):

Coefficient $a_1 \pm \frac{t}{\sqrt{N-2}} \left(\frac{s_{y \cdot x}}{s_x} \right)$, where $t = 1.65$;

$N = 500$ (M) or 493 (F); and $s_{y \cdot x} = \frac{S_y^2 - a_1 S_{xy}}{N}$;

$s_x = \sqrt{\frac{S_x^2}{N}}$.

Regression equations	Range of regression coefficients at 95% confidence limits
Male $TL = 2.34 CL + 39.4$	2.24 - 2.44
Female $TL = 2.40 CL + 47.9$	2.29 - 2.51
Male $AL = 1.34 CL + 32.1$	1.27 - 1.41
Female $AL = 1.56 CL + 17.1$	1.51 - 1.61
Male $TW = 3.29 AW - 3.5$	3.28 - 3.30
Female $TW = 3.15 AW - 20.9$	3.13 - 3.17

Regression equations for total weight (TW) at each abdomen (tail) weight (AW) are useful for converting the "tail" weight of commerce to total

weights for estimates of yields from lobster populations. They are as follows:

Male $TW = 3.29 AW - 3.5$ (N = 500);
 Female $TW = 3.15 AW - 20.9$ (N = 493).

(Figure 5)

In these equations the coefficients have ranges of 3.28 - 3.30 and 3.13 - 3.17 in males and females, respectively (Table 2) so may be considered to be different at the 95% confidence limit. For practical purposes the conversion of tail weight to total weight may be done by a factor of 3.2 if it is known that the numbers of males and females in the catches are equal (Squires, 1974). On the average the tail weight is about 31% and 33% of the total weight in males and females, respectively, or 32% with males and females combined (Table 3).

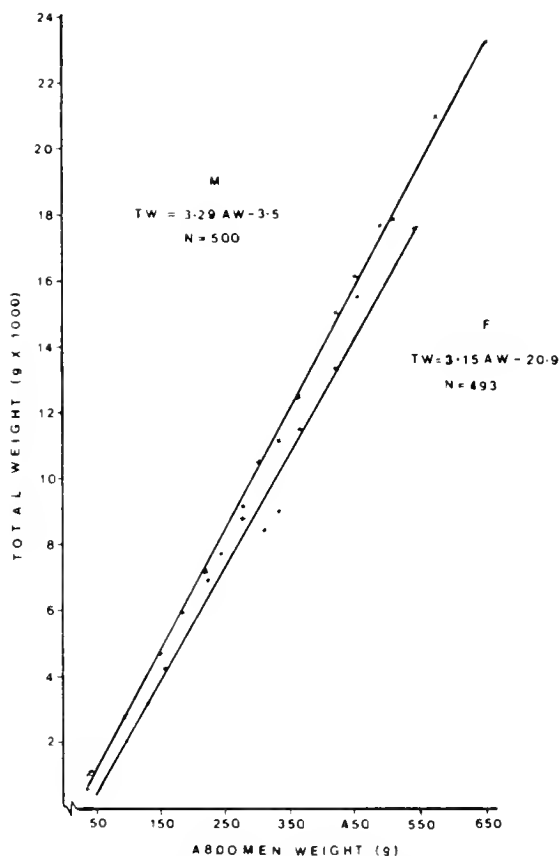


FIGURE 5. Regression of Total Weight (TW) on Abdomen (Tail) Weight (AW) in male and female *Panulirus argus* from the Guajira Peninsula of Colombia.

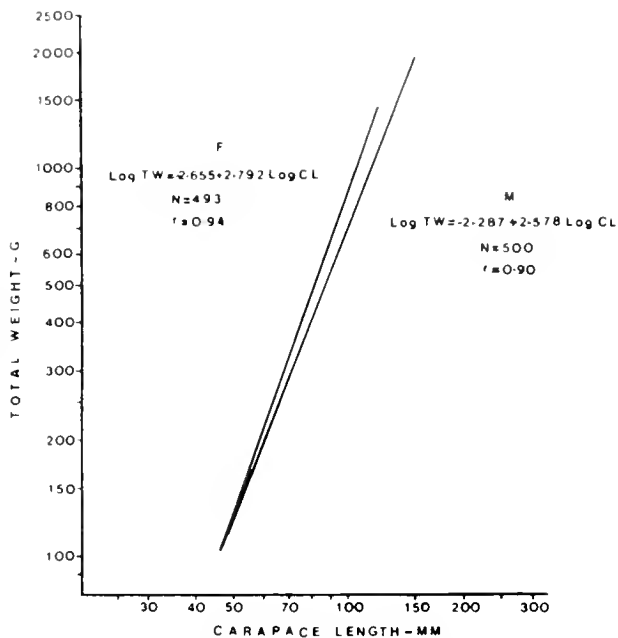


FIGURE 6. Regression of Total Weight (TW) on Carapace Length (CL) in male and female *Panulirus argus* from the Guajira Peninsula of Colombia.

Equations for obtaining total or abdomen weights from carapace lengths (Riveros, 1972) have less practical use. They are as follows:

Male $\text{Log AW} = 2.5146 \text{ Log CL} - 2.6782$
(N = 500);

Female $\text{Log AW} = 2.4331 \text{ Log CL} - 2.4302$
(N = 493). (Figure 7).

Male $\text{Log TW} = 2.5780 \text{ Log CL} - 2.2873$
(N = 500);

Female $\text{Log TW} = 2.7921 \text{ Log CL} - 2.6555$
(N = 493) (Figure 6).

Maturity

Size at first maturity. In females the minimum size of mature lobsters (bearing eggs on the pleopods) was 64 mm CL in these samples. However, the minimum size found with large ova ready to be laid was 55 mm CL, but if this lobster molted before spawning (which is likely) it would be about 61 mm CL when carrying eggs. Only 5% of the females were immature at 71 mm CL and no juveniles or immatures were more than 94 mm CL

TABLE 3. Average abdomen and total weights at average carapace and abdomen lengths in 450 male and 450 female *Panulirus argus* from the Guajira Peninsula of Colombia.

Carapace length mm	Abdomen lengths		Abdomen weights		Total weights		Percent: AW of TW	
	Male mm	Female mm	Male g	Female g	Male g	Female g	Male %	Female %
51	100	97	41	53	131	146	31	36
56	107	104	52	67	168	190	31	35
61	114	112	65	82	210	237	31	35
66	120	120	79	99	256	291	31	34
71	127	128	95	119	309	354	31	34
76	134	136	113	140	368	420	31	33
81	140	143	132	170	431	515	31	33
86	147	151	153	189	500	574	31	33
91	154	159	177	217	579	663	31	33
96	161	167	203	247	664	757	31	33
101	167	175	230	279	757	858	30	33
106	174	182	260	314	852	968	31	32
111	181	190	292	352	957	1088	31	32
116	187	198	326	392	1069	1214	30	32
121	194	206	362	434	1187	1346	30	32
126	201	214	400	479	1319	1530	30	31

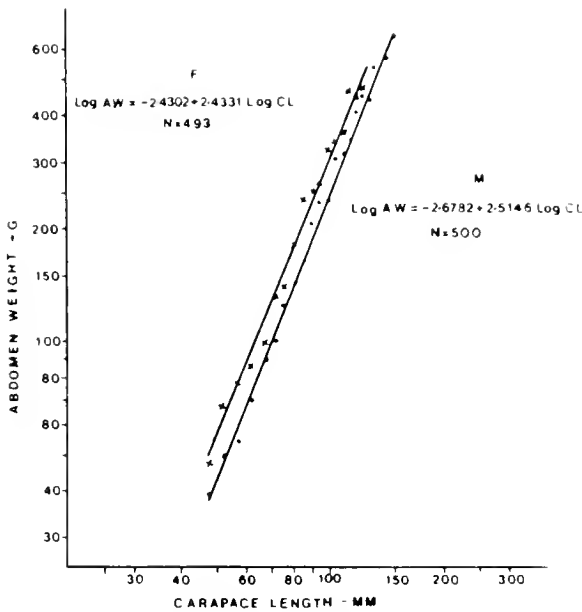


FIGURE 7. Regression of Abdomen (Tail) Weight (TW) on Carapace Length (CL) in male and female *Panulirus argus* from the Guajira Peninsula of Colombia.

(Riveros, 1972). Abdomen widths were greater in proportion to carapace length by about 6% after maturity (Table 4).

In males the smallest matures were 66 mm CL and very few juveniles (5%) were larger than 85 mm CL (Riveros, 1972). The 66 mm CL corresponds to an average tail weight of 79 g or 2.9 oz in males and 99 g. or 3.6 oz in females. Minimum accepted commercial size is a 4 oz (114 g) tail

TABLE 4. Average width of abdomen in female *Panulirus argus* when immature and when mature; expressed as a percentage of CL and TL (total length).

Carapace length mm	Total length mm	Abdomen width as percent of		Maturity
		CL %	TL %	
64	194	78	26	Mature
		72	24	Immature
67	200	75	25	Ovigerous
		69	24	Immature
70	207	71	24	Mature

which would be from a male of 76 mm CL and a female of 71 mm CL. (A minimum size of 76 mm CL was recommended to Government for inclusion in legislation to protect the lobster resource).

Male maturities. After males became mature (with large vasa deferentia purplish in color) they continued to retain full maturity irrespective of season (Riveros, 1972). Maturities could be categorized into three phases (Table 5) with considerable overlap in sizes of specimens.

Female maturities. Four phases of maturity of ova in ovaries (oogenesis) were defined as follows: I, immature or juvenile; II, maturing; III, mature and IV, spent and recovering (Table 6). In all phases there were oocytes or small ova present in the ovarian stromae, but these were beginning to be predominantly orange in color and slightly larger in Phase IV.

Macroscopic phases of embryo development (embryogenesis) in eggs on pleopods could be seen

TABLE 5. Phases of maturity in 500 male *Panulirus argus* from the Guajira Peninsula of Colombia, 1969-70.

Phase	Category	Testes condition and color	Vasa deferentia size and color	Diameter of v.d. mm	Spermatophore glands of 5th legs	Range of CL mm	50% of phase at CL mm
I	Immature	Small, translucent	Small, translucent	>1	Small	40-85	65
II	Maturing	Medium, opaque yellowish	Medium, opaque purplish	1-2	Medium	62-110	83
III	Mature	Large, opaque whitish	Large, purplish	3-4	Large	66-158	100

TABLE 6. Phases of maturity of ova in ovaries (oogenesis) of *Panulirus argus* from the Guajira Peninsula of Colombia, 1969-70.

Phase	Category	Ovary size and color	Oocytes or small ova	Greater diameter of ova mm	Range of CL in category mm	50% of phase at CL mm
I	Immature	Small, whitish translucent or cream to pink	Present, translucent	0.1-0.2	40-90	68
II	Maturing	Orange predominating, but some opaque and whitish	Present, translucent	0.3-0.4	50-105	85
III	Mature	Bright red	Present, translucent or opaque	0.4-0.5	55-130	85
IV	Spent and recovering	Dull reddish orange, few large red degenerating	Not present; small orange ova predominating	0.2-0.3	65-125	85

TABLE 7. *Macroscopic phases of maturity of embryos (embryogenesis) in eggs on pleopods of Panulirus argus from the Guajira Peninsula of Colombia, 1969-70.*

Phase	Category	Color of eggs	Greater diameter of egg mm	Phase of ovary development
I	Full yolk, no eye spot	Bright red	0.5	IV
II	Eye spot a flat black crescent	Orange	0.6	II
III	Eye spot round, limb structure visible; prenaupliosoma	Brownish	0.7-0.8	III

under low magnification (10X). Three phases were defined: the first in which no eye spot was present, the second with the eye spot merely a slit or black crescent and the third when the eye spot was rounded and limbs of the prenaupliosoma could be distinguished (Table 7). These phases corresponded with Phases IV, II and III, respectively, of ovarian development indicating that by the time embryos were ready to hatch the ova were almost ready to be extruded. In a very few large females carrying eggs the ovaries showed only an early phase of development. Incidentally, the early phases of embryo development in eggs on pleopods were seen more frequently than the later phase (Table 8).

Abdomen width as an indication of maturity. Immature females had narrower abdomens than mature females of the same CL. As a percentage of CL average abdomen widths were about 67% in

TABLE 8. *Incidence of macroscopic phases of embryo development (Table 6) in samples of Panulirus argus (August, 1969 to May, 1970) from the Guajira Peninsula of Colombia.*

Month	Phase I	Phase II	Phase III	Number examined
	(red) %	(orange) %	(brown) %	
Aug	67	19	15	27
Sept	64	14	21	14
Oct	64	36	0	14
Nov	-	-	-	-
Dec	50	36	14	14
Jan	-	-	-	-
Feb	100	0	0	3
Mar	0	0	100	1
Apr	-	-	-	-
May	67	0	33	3

immature and 72% in mature females. In the 234 females included in this comparison the change from immature to mature abdomen widths occurred at about 70 mm CL (Table 4).

Fecundity. Counts of eggs from 19 females from these samples by Herazo (1971) gave average numbers of just over 300,000 at a size of 75 mm CL and more than one million at 110 mm CL (Figure 8).

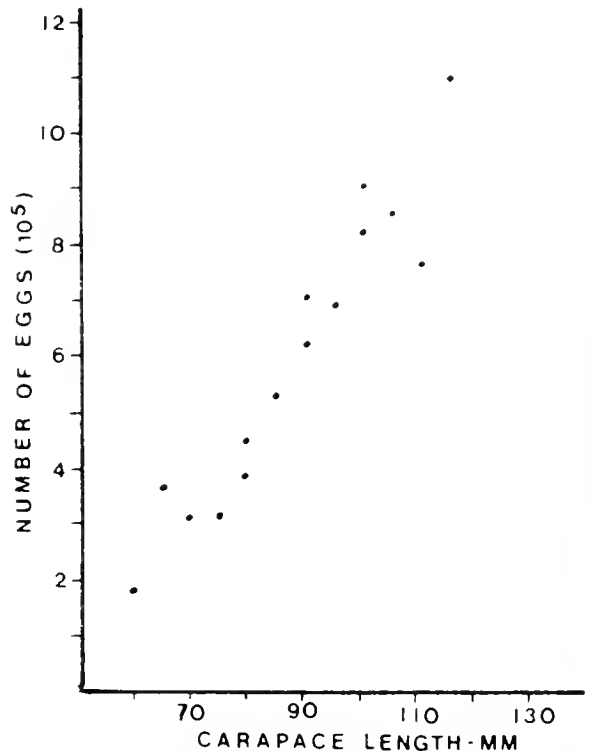


FIGURE 8. *Number of eggs at each Carapace Length (CL) in Panulirus argus from the Guajira Peninsula of Colombia (Counts of eggs from pleopods of 19 females).*

Stomach contents

Of the 93 stomachs examined (only those with food are included) 40 percent contained fish remains (bone and tissue fragments). Crustacean remains (fragments of crabs and shrimps) were in 30% of the stomachs, and molluscan shells (bivalves and gastropods) in 20%. The rest comprised low incidence of fragments of echinoderms and plants. Sand was present in small quantities in all. Molluscan shells and echinoderm remains were frequently seen in intestines but only stomachs were examined in detail.

Shell condition

The highest percentages with new shells were in May (18%), July (6%) and September (10%). In other months the percentages varied from 1-6% (Table 9).

Temperature and salinity

Average water temperatures on the fishing grounds were 27 C from 1-10 m deep and 24 C from 10-20 m during periods of observation (Squires et al., 1974). Salinities observed were 34-37‰.

TABLE 9. *New shells in monthly samples of Panulirus argus from the Guajira Peninsula of Colombia, 1969-70.*

Month	Percent with new shell %	Number examined
May	18	164
June	0	10
July	8	68
Aug	3	91
Sept	10	143
Oct	8	72
Nov	-	-
Dec	1	69
Jan	0	21
Feb	1	73
Mar	0	21
Apr	-	-
May	8	195
Average	5	Total 927

ESTIMATE OF YIELD AND DENSITY OF SPINY LOBSTERS ON THE FISHING GROUNDS

A comparison of landings from trap fishing and from diving indicates that in 1971 and 1972 the divers contributed more than 85% to the landings (Figure 2). In the month to month fluctuations in landings September-November and March-June produced 8,000-16,000 kg a month while July and August had less than 3,000 kg and December the least with only 1,500 kg (Riveros, 1972). These fluctuations were reportedly the results of changes in fishing effort because of weather conditions or tribal activity of the Guajiros.

Fishing with traps, operated over an area of approximately 40 km² near Riohacha (about 20 km by 2 km), caught about 20,000 kg in 1971. About 200 traps were hauled daily with not less than three days between hauls for any one trap. The maximum traps in use was 1,000. Catch per area was:

$$\frac{20,000 \text{ kg}}{40 \text{ km}^2} \quad \text{or} \quad 500 \text{ kg per km}^2.$$

Assuming that lobsters could have been obtained from a total area of potential fishing grounds between depths of 5 and 45 m (conservatively 2,000 km² in area) between Cabo de la Vela and Camarones (Figure 1), the annual yield would be about 1000 tons. The total catch in 1971 was reported as 540 tons (tail weight = 170 tons).

From a potential yield of 1,000 tons and an average weight of about 400 g for each spiny lobster at commercial sizes, the density of lobsters on the grounds would be about 1 to every 400 m². This estimate is obtained from the total number of commercial lobsters in 1,000 tons (about 2,500,000) plus an equal number of pre-commercial sizes, and assuming that they were all evenly distributed over the shelf area.

DISCUSSION

The fishery

Although the average catch of fishermen using traps off Riohacha was approximately 2 tons each it did not exceed the average catch of the Amerindians diving for lobsters. The latter do not have a strong incentive to catch more. Their need for cash income is more than satisfied by the rate of fishing, and they fish only when there is no fiesta

or other tribal activity. Although their "free" diving (with face mask only and with no fins) is relatively effective compared with trapping, they cannot dive during windy weather when the sand is stirred up and visibility is low in the water and sharks are more dangerous. Trapping would reduce the hazards. The investment in larger boats and traps, however, would require a much larger catch to provide the same level of income to these fishermen.

Fishery regulations prescribe a minimum size, a "veda" or closed season and non-retention of egg-bearing females. Because several market outlets are available, the Guajiros sell only to buyers who will take all sizes of lobsters. The closed season is not observed. There is, however, a natural season all but closed to the divers during about three months of heavy winds, and since there are uniformly warm water conditions throughout the year, there is no season such as a breeding season when closure would be useful. Also, since most adult females are either carrying eggs or ready to lay eggs, saving the egg-bearing ones would not be different from saving the non-egg-bearing. The only regulation, therefore, that would be useful is the one related to minimum size which would add appreciably to the total weight of lobsters harvested each year if kept strictly (Table 10). A minimum size suggested is 76 mm CL which could be increased in subsequent years if accepted by the fishermen.

Weight gains per molt.

Hypothetical weight gain per molt may be estimated from average weights at given carapace

lengths when the increment in length with each molt is known (Squires, 1970; Squires et al, 1971; Riveros, 1972). The average molting increment of 8 mm CL estimated by Riveros (1972) may be excessive in view of the estimates given by others for this species. Munro (1973) reviewing several works from different areas suggests 30 mm per year in four molts; Peacock (1974) for Antigua and Barbuda, 21-35 mm in 4-5 molts and Beaumariage and Little (1975) 15 mm, presumably in two molts in Florida. Olsen et al (1972) documented slower growth in females than in males: 4-7 mm per molt compared with 4-8 mm. In this paper, 6 mm increments in CL per molt in males and females is taken for calculations of weight gains (Table 10).

Starting at 59 mm CL (178 g) weight gains of males would be 35% in one, 63% in two, 105% in three and 142% in four molts. Corresponding gains in females would be 39%, 74%, 111% and 159% of the original weight of 190 g at 59 mm CL. Percentage gains in abdomen weight were slightly less (Table 10). Olsen et al (1972), however, postulates that molting in females is less frequent than in males so that increases in weight would take place over a longer time.

Demonstrating weight gain in lobsters (if left to molt) is a way to convince fishermen how much weight is lost to a fishery if lobsters smaller than regulation size are taken. Also it shows them that small lobsters will soon gain weight if left on the grounds where they may be caught again later after release.

TABLE 10. *Hypothetical gains in weight of male and female Panulirus argus using average CL increments of 6 mm in each molt and an original CL of 59 mm (Calculated from regression equations of total weight (TW) and abdomen weight (AW) on carapace length (CL)). (Figures 6 and 7).*

CL mm	Average total weights		Average abdomen weights		Percent gain on original weight			
					Total weights		Abdomen weights	
	Male g	Female g	Male g	Female g	Male %	Female %	Male %	Female %
59	178	190	70	85				
65	240	265	87	107	35	39	25	26
71	290	330	100	126	63	74	43	48
77	365	400	121	147	105	111	73	73
83	430	490	138	174	142	159	97	104
89	515	600	162	206	189	216	131	142

Reproductive potential.

Chittleborough (1974) found that individual mature females of *P. longipes cyngus* spawned approximately every second month when kept in aquaria under high temperature conditions similar to those prevailing in tropical areas. Berry (1971) also noted repeated spawnings of *P. homarus* approximating once every two months while the warm temperatures of summer prevailed in South Africa. Squires (1973) suggested that reproductive cycles under tropical conditions were short, and that spawning in mature female lobsters of the Guajira occurred every 2.5 months throughout the year. Olsen et al. (1972), from direct observations of female *P. argus* in the Virgin Islands during underwater studies, remarked that "females may reproduce several times a year".

During the present investigations the completion of development of embryos in eggs (embryogenesis appeared to be approximately equal to the development of ova in ovaries (oogenesis). Also, the monthly percentage of mature females carrying eggs was frequently in excess of 50% (seven times out of eleven), and the average percentage was 50% in the eleven samples examined (Table 11). Although data were obtained from fairly small numbers and samples were not obtained in some months, every second month of 1970-71 had the greater percentage carrying eggs (Table 11). Since the samples were taken almost exactly one month apart and from approximately the same area, the effects of synchrony in bi-monthly spawning might be indicated from these data. Apparently most mature females spawned every second month.

New shells.

Although an average of only 5% of shells examined appeared to be new, some were present in most months (Table 9). The low percentages may have been caused by the following: the inability of the examiner to recognize new shells, the selection by divers against soft shells, discarding of injured soft-shelled lobsters before bringing to the factory and possibly by recently molted lobsters being more secretive in behaviour. As indicated by Chittleborough (1974), it is likely that molting followed hatching of larvae from the eggs, and preceded egg-bearing. Where spawning was frequent,

TABLE 11. Percent of mature female *Panulirus argus ovigerous* in monthly samples from the Guajira Peninsula, Colombia, 1969-70.

Months	Percent ovigerous %	Number of Mature females examined
Apr	66	29
May	49	35
June	63	8
July	-	-
Aug	73	44
Sept	56	43
Oct	73	40
Nov	-	-
Dec	40	35
Jan	18	11
Feb	53	27
Mar	27	11
Apr	-	-
May	23	64
Average	50 Total	347

therefore, lobsters with new shells would be present in all months. In the first six months of this study (May-October, 1969) each alternate month had a higher percentage of new shells (Table 9). This appeared to correspond with the months following those in which peaks of spawning occurred (Table 11).

ACKNOWLEDGEMENTS

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ABSTRACTS OF THE TECHNICAL PAPERS PRESENTED AT THE 1977 NSA CONVENTION

MEXICAN MOLLUSCAN FISHERIES OF THE GULF OF MEXICO AND THE CARIBBEAN : 1970-1975

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Molluscan fishery statistics for the Mexican Gulf and Caribbean have been analyzed for 1970-1975 for each molluscan group or by-product landed, and for each of the six coastal states. The statistics listed the landings by the following "classes" of molluscan groups or by-products: sea clam, river clam, squid, mixed shells (industrial), conch meats, mixed molluscan meats, oyster with shell, oyster meats and octopus. During 1970-1975 total molluscan landings of 189,131 metric tonnes, valued at \$29,637,244 (USA), were reported for the area—averaging about 31,522 tonnes, worth about \$4,939,541 (USA), per year. The most important molluscan fishery of the region during the period was for "oyster with shell" (mainly *Crassostrea virginica*), followed far behind by the octopus fishery (*Octopus vulgaris* and *O. maya*.) The oyster with shell fishery represented about 84% by weight and 50% by value of total molluscan landings, including by-products, from the Mexican Gulf and Caribbean region during 1970-1975. The octopus fishery represented 8.3% by weight and 25.1% by value of total molluscan landings. Veracruz was by far the most important state for molluscan landings. During the period, 51.8% of the total weight of landings, and 31.9% of total value, from the region were reported from the state of Veracruz. The state of Tabasco was se-

cond in total weight landed (29.5%) and the state of Campeche was second in total value of landings (23.1%) for the entire region.

A DISEASE SURVEY OF NEW ENGLAND SOFT-SHELL CLAMS, *MYA ARENARIA*

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A field survey for possible pollution-related diseases of the soft-shell clam was initiated in January, 1976. To date, more than 1500 clams from 10 sites of differing types and degrees of pollution have been histopathologically examined. Lesions noted included: disturbances of growth (neoplasia, hyperplasia, hypoplasia), reaction to injury (hemocytosis, inflammation), presence of parasites (bedsonia, protozoan, metazoan, and accumulations of orange-brown pigmented bodies (both intra- and extracellularly).

The prevalence of these lesions varied between sites suggesting environmental influences. Cytologic examination, coupled with a significantly increased mortality during a 10 month study indicated the malignancy of the neoplastic disease.

HISTOCHEMICAL ANALYSES OF PIGMENT ACCUMULATIONS IN *MERCENARIA MERCENARIA* L. AND *MYA ARENARIA* L.

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Histopathologic analysis of *Mercenaria* collected from Massachusetts, Rhode Island and New Jersey demonstrated accumulations of pigments of three types: 1) irregular, 2-20 μm diameter, orange-brown staining (H&E) bodies, present extracellularly in the alimentary tract epithelium and gonadal connective tissue, and intracellularly in renal epithelium; 2) spherical 7-12 μm diameter eosinophilic concretions, present intracellularly in renal epithelium; and 3) 30-200 μm diameter melanotic casts present in renal tubular lumens.

Only type 1 pigment was found in *Mya* collected throughout New England, and was present in lesser amounts than in *Mercenaria* from adjacent locations. This pigment had morphological characteristics of lipofuscins (brown staining bodies of oxidized lipids) found in vertebrates. All three pigment types had histochemical characteristics of lipofuscins.

Based on the examination of over 200 *Mercenaria* and 1500 *Mya*, the accumulation of these pigments appears to be a normal physiological process, although abnormally large accumulations were noted in clams from certain environments.

CULTURE OF HATCHERY-SPAWNED *MERCENARIA MERCENARIA* IN MASSACHUSETTS

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Coastal towns, which have the prime responsibility for managing shellfish in Massachusetts, are finding hatcheries to be one of the best sources for hard clams (*M. mercenaria*). During 1976, 12 towns bought hatchery stock between 5-14 mm (longest diameter). A variety of on-bottom and off-bottom systems was used to isolate the clams from predators. Growth varied with system de-

sign, density of clams, and substrate type. Survival prior to winter, though 90% or more, must be qualified. During the winter, survival was 80-90% in rafts and widely variable in pens lying in intertidal and shallow subtidal areas. The success of most transplants into natural, unprotected bottom appears related to the number of green crabs observed in the transplant site. Although the theoretical yield of this technique is high, the actual benefit to a town management program remains to be proven.

ULTRASTRUCTURAL EVIDENCE THAT GASTROPODS SWALLOW SHELL RASPED DURING HOLE BORING

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Observations are reported on the ultrastructure of shell material rasped by *Urosalpinx cinerea follyensis* Baker from boreholes in the valves of *Mytilus edulis* Linne and transported normally to the stomach through the buccal cavity and esophagus. Duration of the period of chemical activity by the accessory boring organ and rasping by the radula were determined with a valve model. Pellets of shell raspings were removed from the stomach and, after fracturing to reveal the interior, and coating with metal, were studied with the scanning electron microscope. Shell raspings were compared with prisms and lamellae in fracture surfaces of normal shell of *M. edulis* and shell etched with ethylenediamine and sodium hypochlorite to reveal the form of shell units clearly.

The study provided ultrastructural evidence for the first time that *U. cinerea* swallows shell rasped from the borehole during penetration of prey. Both prisms and lamellae were identified in the pellets removed from the stomach. Noticeable dissolution of the organic matrix, and to some extent also of the mineral portion, of prisms was evident, features which facilitate removal of shell by the snail during rasping. If the long axis of prisms occurs parallel to the surface of the borehole, the radula tends to rasp out long fragments of shell; if prisms are placed at right angles to the surface, the

radula breaks prisms into small pieces. The envelope of mucoid material which coats pellets undoubtedly reduces, or prevents, laceration of the epithelium of the alimentary canal as shell fragments pass down the tract. A gross approximation of the percentage of shell in the borehole which is rasped and swallowed during the process of hole boring is 14%.

THE INTERACTION OF WATER SOLUBLE
FRACTIONS (WSF) OF SOUTH LOUISIANA
CRUDE OIL AND *DERMOCYSTIDIUM*
(*LABYRINTHOMYXA*) *MARINUM* AT
VARYING TEMPERATURES IN THE
AMERICAN OYSTER,
CRASSOSTREA VIRGINICA GMELIN

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Over 500 oysters infected with *D. marina* were exposed to 100% WSF crude oil in closed seawater systems with water temperatures varying between 16°- 28° C. Elevated water temperature resulted in greater mortality and significantly higher levels of *D. marina* in infected oysters. Oysters exposed to the WSF had significantly greater mortality and decreased levels of *D. marina* than non-exposed oysters. Concomitant temperature elevation and exposure to WSF significantly increased mortality and the rate of uptake of naphthalenic hydrocarbons.

TETRACYCLINE AS A BIVALVE
SHELL MARKER

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Crassostrea virginica, *Mercenaria mercenaria* and *Mytilus edulis* were exposed to the antibiotic tetracycline in ambient sea water. The antibiotic was dissolved in filtered sea water, to which algal food was added. The animals were allowed to feed on this mixture, which encouraged rapid shell growth. The marking period lasted one week to several months. Tetracycline was incorporated concurrently with the rapid deposition of new shell. The inlaid tetracycline fluoresces a vivid yellow-orange under UV light (Mineralight, 254nm). Marking was vivid in *Crassostrea* and *Mercenaria* and vague in *Mytilus*.

Marking was vague at 0.5 and 5.0 mg L⁻¹ but vivid at 25 to 200 mg L⁻¹. No deaths or morphological defects were noted at any concentration tested. The amount of inlaid tetracycline was related to the quality of algal food. Algae species known to be good food sources produced the greatest incorporation of tetracycline. Marking of *Mercenaria* larval and spat shells was visibly bright at 25 and 50 mg L⁻¹ and visibly evident at 0.5 and 5.0 mg L⁻¹. under the dissecting microscope. Experiments with five tetracycline analogues showed that tetracycline phosphate complex produced the best results with tetracycline HCL, oxytetracycline, doxycycline and minocycline producing progressively poorer results.

The mark remains undiminished *in vivo* for at least seven months, and its permanence is suggested by structural changes to shell crystals on the ultrastructural scale. The persistence of the mark and its distinctive fluorescence suggest the utility of tetracycline in studies of shell growth and morphology and in field investigations. Commercially, this technique could be used as an identification, for example, by hatcheries to combat poaching on leased grow-out grounds.

OYSTER REEF CULTIVATION
FOR CULTCH MATERIAL

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A modified oyster dredge was used as a method of utilizing existing buried shell for cultch. SCUBA

and random m² quadrats were used before and after dredging to sample Bayou Cour Reef, Kings Bayou Reef, and Shellbank Reef in Mobile Bay and Bon Secour Bay, Alabama. The reefs were dredged at a rate of 6.4 km/hour covering 0.4 ha in one hour and 15 minutes.

The modified dredge was found to destroy half-shell while exposing the half-shell resulting in an increase in shell weight. The bottom was disrupted and the exposed shell appeared to settle into the bottom with a subsequent loss of relief followed by an accumulation of silt.

Spat set increased following dredging, but loss of relief makes this method unsatisfactory for reefs over a soft substrate. Man-made or rehabilitated oyster reefs on hard substrate may benefit from this method.

MARKING CLAMS WITH RUBIDIUM¹

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Hard shelled clams, *Mercenaria mercenaria*, were successfully marked with rubidium by rearing seed clams in artificial seawater with an aqueous solution of rubidium chloride. Elevated levels of Rb⁺ in samples of tissue were detected by atomic absorption spectroscopy. Clams exposed for 48 and 96 hours to 10.0, 1.0, 0.1 and 0.01 g/l RbCl contained levels of Rb⁺ significantly higher than endogenous levels. Biological activity, measured as siphon extension and survival of clams, was not affected by the presence of RbCl at concentrations less than 10.0 g/l. Also, significantly higher levels of Rb⁺ were present in tissue for up to 3 weeks when clams were exposed to 1.0 g/l RbCl for 96 hours then transferred to uncontaminated water.

Diatoms, *Phaedactylus tricorutum*, exposed for 24, 48 and 96 hours to 10.0, 1.0 and 0.1 g/l RbCl had significantly higher levels of Rb⁺ than diatoms cultured without RbCl. Clams cultured for 96 hours in vessels containing diatoms exposed to 1.0 g/l RbCl had significantly more Rb⁺ than

clams grown with unlabelled diatoms. Clams exposed to 1.0 g/l RbCl solutions with and without diatoms contained levels of Rb⁺ significantly higher than those clams reared only with labelled diatoms. No significant difference was detected between clams grown with and without diatoms at 1.0 g/l RbCl.

Mud crabs, *Panopeus herbstii*, were offered Rb⁺ labelled clams for 96 hours then sacrificed or transferred to containers with unlabelled clams for 7 days. Control crabs were fed unlabelled clams and sacrificed at 96 hours and 7 days. Fecal strands of experimental crabs had elevated levels of Rb⁺ with a peak at approximately 132 hours. Four tissues dissected from control and experimental crabs were analyzed and significantly higher levels of Rb⁺ were found in the hepatopancreas of experimental crabs after the first 96 hours. No apparent difference was detected at 7 days.

¹ This study was supported by the South Carolina Experiment Station and Clemson University Faculty Research Committee.

SUSPENSION CULTURE OF EUROPEAN OYSTERS (*OSTREA EDULIS* L.)

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Operations have appeared along the coast of Maine during the past few years for the culture of European oysters. Suspension techniques are used for the grow-out of cultchless, hatchery-reared seed, and suspension systems most often involve one or another variation on the Japanese long-lining theme. The first system to appear commercially employs floating modules consisting of stacks of wooden-framed plastic mesh trays short-tethered to a long hauser line. These are tended from a raft which can hoist modules aboard for servicing—cleaning, grading, etc.—one at a time. A second system was recently introduced which makes use of culture nets imported from Japan where they were developed for the rearing of pearl shells and scallops. In this system the gear is in-

dividually buoyed and suspended, either near the surface or at mid-depth, beneath a long line. A service raft is also utilized and in this case there exists the possibility of batch-servicing a number of net modules simultaneously. A third technique has appeared for nursery grow-out in well protected areas. The culture unit is a rectangular, wooden-framed tray enclosed with plastic mesh on both top and bottom. These are strung together end to end, floated in rows, and flipped regularly so that each side is alternately exposed and submerged, a procedure which controls fouling. The equipment and methods of several oyster farms are illustrated and discussed indicating the varying approaches to common problems such as retrieval and resuspension of modules, prevention and removal of fouling, overwintering and others. The development of the Maine oyster aquaculture industry as a whole is briefly reviewed.

GROWTH RESPONSES OF EUROPEAN
AND AMERICAN OYSTERS
(*OSTREA EDULIS* L.
AND *CRASSOSTREA VIRGINICA* G.)
TO INTERTIDAL EXPOSURE

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In view of the use which is made of the intertidal zone in the rearing of oysters in other areas of the world (e.g., Japan, New Zealand) studies were undertaken to determine its potential usefulness to the culture of European and American oysters in Maine. As part of a seed "hardening" experiment, spat were suspended at 1 subtidal and 5 intertidal levels (9-49% mean aerial exposure time). Monthly instantaneous growth (whole dry weight) rates (k) indicated American oysters to be "breaking even" with exposure; i.e., over the range of levels tested a given percentage change in immersion times was matched by an equal change in k so that growth relative to immersion time was approximately the same at all levels. The k vs. exposure curve for European oyster seed was also linear but differed in having a more rapid decline in growth with increasing exposure. A similar pat-

tern of growth was exhibited by yearlings of the 2 species suspended for 5 months at 10 levels centered more or less on mean low water. Because of the closer spacing and more restricted range of exposure levels (0-30%) in this experiment, however, a better resolution of the growth response at the lower levels of exposure was possible, and an interesting feature of European oyster growth not distinguishable in the seed study emerged: Growth at levels of exposure up to 10-12% equalled that of subtidal oysters, indicating that growth relative to immersion time was actually greatest in the groups exposed at low levels. At higher levels k values declined rapidly. Growth of American oysters again appeared to correspond with immersion time in a one-to-one fashion. The *O. edulis* result suggests a potential use of the lower intertidal for the "market hardening"—conditioning for prolonged valve closure—of European oysters to extend their shelf life, a problem which has been troubling Maine aquaculturists. Such a procedure need not entail any loss of growth.

THE ONSHORE SURF CLAM RESOURCE
ALONG THE SOUTHERN NEW JERSEY
COAST

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With the general decline of the offshore surf clam beds under increasing dredging pressure over the past decade, an increasing proportion of the New Jersey catch has been taken from the inshore beds, close to the beaches of Atlantic and Cape May Counties. This shift in fishing effort has caused concern for the maintenance of the inshore populations and, since 1972, has led to studies of population size, distribution, recruitment and growth.

During this period the standing stock within the three-mile limit has been declining continuously and is now estimated at less than 4-million

bushels. In general the more dense populations are close to the beaches and, within the three-mile limit, decrease in density with distance offshore. The clams also show two distinct gradients in size: (1) smaller clams inshore; (2) smaller clams up the shore in the stretch from Cape May to Beach Haven inlet.

Over several summer seasons settling of juveniles has been general in the inshore area with densities ranging up to several hundred per square meter. Early mortality rates, however, have been high and by end of summer young of the year are virtually non-existent. Principal predators include *Limulus*, *Ovalipes* and *Pagurus*. No substantial recruitment has occurred in the past five years.

MORTALITY PATTERNS AND DISEASE RESISTANCE IN DELAWARE BAY OYSTERS

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Since 1964, 20 groups of oysters have been laboratory-bred for resistance to kill by *Minchinia nelsoni*, then selected and tested for survival in enzootic waters in Delaware Bay. Survival at the end of a 33-month test period of four filial generations of selected stocks has been compared to that of unselected groups. Compared to 16 groups of susceptibles the survival ratio of F₁ resistants is 4.4; this ratio increases to 5.0, 6.6 and 8.9 for F₂, F₃ and F₄ respectively. Native set originating from parents selected on planted grounds in the lower bay, have a cumulative kill falling between susceptibles and F₁ resistants, with a survival ratio of 2.9 compared to the unselected stocks.

Differential mortality ratios are established during exposure to the first complete summer infective period and are maintained with little variation for the remainder of the test period. Despite a plateauing of cumulative mortality curves for all stocks after the initial kill, seasonal mortality rates remain higher for susceptibles than for resistant groups after nearly three years of selection.

Non-predation kill on Delaware Bay native seed stocks planted on low bay leased grounds during the past 12 years has generally demonstrated survival comparable to laboratory-reared resistant groups.

THE OYSTER INDUSTRY OF VIRGINIA 1931 to 1975

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This study investigates the cause or causes of the decline in productivity of Virginia's oyster industry over the years and especially the catastrophic decline since 1960. Included in this report are detailed studies on landings and oyster density, a documentation of the decline in spatfall in many areas since 1960, reviews of predators and diseases, repletion activities, laws and other aspects.

The principal reason for the decline since 1960 has been the direct or indirect impact of MSX, but other factors associated with degradation of the environment may also have operated. In many instances rising labor costs and antiquated technology have prevented a recovery of the industry.

Recommendations for improving the industry are given.

AGE, GROWTH, REPRODUCTION AND DISTRIBUTION OF THE BAY SCALLOP, *AEQUIPECTEN IRRADIANS IRRADIANS* (LAMARCK), IN THREE EMBAYMENTS OF EASTERN LONG ISLAND, NEW YORK, AS RELATED TO THE FISHERY

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Bay scallops are an economically important fishery on eastern Long Island. The bay scallop

populations in three embayments in the Town of East Hampton, N.Y., were studied for weight, growth, and condition of the adductor muscle, reproduction, shell growth, abundance and distribution.

The spawning effort is maximized at the expense of other functions. Spawning occurs primarily in June and is temperature related. The adductor muscle index and condition decrease during gonad maturation and spawning, and shell growth nearly ceases during the reproductive period. The greatest rate of weight gain of the adductor muscle and greatest shell growth occur during the post-spawning period, July through October.

Commercially acceptable growth appeared to be density and depth related. Modal shell length of the harvestable year class was 60-65 mm at the beginning of the fishing season in October. State and local minimum size regulations were evaluated on a biological basis and management recommendations were discussed.

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OYSTER SETTING - EVOLUTION OF COMMERCIAL HATCHERY TECHNIQUE

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Cultchless setting has obviously revolutionized hatchery economics. Bill Budge's development has led to a variety of proprietary and apparently non-proprietary approaches to the process. Ultimate optimization in cultchless setting must depend on a complete understanding of physiological and behavioral responses at setting. It is clear that oyster larvae can delay metamorphosis and set in response to environmental stimuli. Our experiments indicate that the setting response is released by rapid temperature increases, water-borne pheromones from adult oysters, and an unknown property associated with calcium carbonate of shell. All are used to advantage in an ef-

ficient cultchless process. Several calcium carbonate related materials appear to be stimulatory including tropical beach sand, foraminiferal sand (we thank Mr. Thomas W. Dignes for suggesting the use of foraminiferal sand as a cultch material), polished marble and marble chips. It is possible to orient larvae with hinge-side uppermost on vertical polished marble slabs thus increasing the efficiency of removal without damage. A complete understanding of the response to calcium carbonate may allow us a system of oyster metamorphosis in the absence of substrate.

AN OYSTER FAMILY TREE: ANCESTRY OF *CRASSOSTREA VIRGINICA*

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A hypothetical family tree of oysters is presented, based on the authoritative text of H.B. Stenzel ("Oysters," volume 3 of 3, Part N, Bivalvia, Mollusca 6, Moore's Treatise on Invertebrate Paleontology, 1971). However, I do not believe that our oyster descended from the giant Eocene "*Crassostrea*" *gigantissima* as some geologists argue (Sohl and Kauffman, 1964, and others). As an ancestor for our oyster I prefer *Crassostrea glabra* (Meek and Hayden, 1857). This species was abundant in widely separated parts of the huge brackish Laramie Sea that extended across the interior of Western North American, from Canada to Mexico, in very late Cretaceous time. It was associated with a few other species of marine origin (species of *Anomia*, *Brachidontes* and *Corbula*, along with some species of genera which have both marine and fresh-water affinities: *Corbicula*, *Neritina*, *Melania*, and other). In other parts of the same sea there were many species of genera which are now found only in fresh water, indicating that salinity must have been very low. *C. glabra* seems to have been a true *Crassostrea*, usually lacking the marginal denticles that Stenzel called "chomata," and was very similar to living Maryland oysters of

the deep-water type. Descent from an oyster of a low-salinity brackish sea may account for the fact that *C. virginica* tolerates lower salinity than any other living oyster. *C. gigantissima*, besides having chomata when young and thus not being a *Crassostrea* by Stenzel's definition, was associated with many marine species as you would expect if it grew in salty coastal lagoons.

BACTERIOLOGICAL STUDIES OF LONG ISLAND SHELLFISH HATCHERIES¹

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High concentrations of bacteria in shellfish hatchery media have been reported as a cause of larval mortality. This study was undertaken to characterize the dominant bacterial flora of the Long Island shellfish hatcheries. Although the study was initiated at a single hatchery during 1972, the current report covers a three-year period (1974-1976) and includes 5 hatcheries. Bacteriological samples from sick and healthy oyster and clam larval cultures and their ingredients were taken at a standard working dilution onto Plate Count Agar media with synthetic sea salts. Each cultural sample was replicated in triplicate. The hatchery ingredients samples included incoming ultraviolet treated and untreated bay and well water, stock algal cultures, and pooled algal cultures. Samples were taken throughout the year at regular monthly intervals. Qualitative and quantitative counts were made of the dominant populations of each culture and isolated colonies were identified as pure cultures.

A total of 1,279 cultures were taken and 710 pure bacterial isolates were identified. Sixty-six percent of all bacteria isolated and identified from intake water samples were gram negative, and 15.7 percent were gram positive. Well water had a higher percentage of gram positive organisms than did bay water intake. Thirty-three percent *Pseudomonas*, 10.4 percent *Flavobacter* or *Cytophaga*, 8.7 percent *Acinetobacter*, 4.9 percent *Aeromonas*, 3.8 percent *Enterobacteriaceae*,

3.2 percent *Vibrio* and 1.5 percent *Achromobacter* spp. were the dominant gram negative isolates found in all water sampled. Well water counts were lower but contained a higher percentage of *Aeromonas*, *Vibrio*, and *Flavobacter* or *Cytophaga* and less *Enterobacteriaceae* than did bay water. Ultraviolet treatment had no effect on bacterial counts of hatchery water intake. Stock algal cultures were frequently contaminated with a wide variety of bacteria. The percentage of *Acinetobacter* and *Flavobacter* or *Cytophaga* spp. increased in algal cultures. Sick or dying oyster larval cultures are characterized by a sharp decrease in the percentages of *Pseudomonas*, *Flavobacter* or *Cytophaga*, *Acinetobacter* and *Enterobacteriaceae* spp. and a rise in percent gram positive bacteria. Sick clam larval cultures were associated with a drop in the percentage of *Flavobacter* or *Cytophaga*, *Aeromonas*, and *Enterobacteriaceae* spp. The percent of unidentified and lost bacterial cultures increased in sick oyster and clam larval cultures. Each hatchery larval culture media had its own distinctive bacterial flora. High bacterial counts were associated with warm weather, increased storage and culture time, and high organic content. The frequency and distribution of *Vibrio* spp. during an outbreak of vibriosis is reported. Water quality studies were conducted during the study. The usefulness of routine bacteriologic sampling for diagnostic purposes is discussed.

1. 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.

WATER QUALITY STUDIES OF LONG ISLAND SHELLFISH HATCHERIES¹

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Since the health of shellfish larvae and the efficacy of shellfish hatchery production is depend-

ent upon the characteristics and stability of the water supply, a study of the water quality of bay and well water intakes of 5 Long Island shellfish hatcheries was undertaken to define the cycle and range of water quality changes throughout a production year. Samples were taken at regular monthly intervals and included measurements for ammonia, nitrate, nitrite, orthophosphate, total organic phosphate, total inorganic phosphate, dissolved oxygen, pH, salinity and temperature.

Ammonia well values ranged from a low of 0.5 to a high of 5.2 and a mean of 1.67 mg/liter. Bay intake ammonia values ranged from 1.7 to 7.0 and a mean of 4.52 mg/liter through the year. Ammonia values rose through the spring and summer months with a sharp decline at the end of the year during early winter. A precipitous short-term drop in ammonia levels in July was associated with an outbreak of vibriosis and high larval mortality at one hatchery.

Nitrate values ranged from 0.5 to 5.0, mean 1.77 mg/liter for well; and 0.5 to 6.1, mean 4.52 mg/liter for bay intake. During spring and summer months low levels of nitrate were found, followed by a sharp increase in fall and winter.

Orthophosphate levels ranged from 0.03 to 0.095, mean 0.05 mg/liter for well water and 0.04 to 0.40, mean 0.186 mg/liter, for bay intake. In the presence of oxygen, orthophosphate and iron levels are interrelated. An extremely high short-term orthophosphate level was associated with disease at one hatchery utilizing fossil fuel thermal effluent.

Iron levels in bay water increased markedly in the spring of the year and decreased later. Iron levels in well water were low and at a stable level. Copper fluctuated throughout the year, but were always higher than reported for ambient oceanic levels.

Well intake had lower pH values than bay intake. Both became more alkaline during spring and summer, and more acid during fall and winter months.

More work is needed to select and define the criteria for water quality tests at shellfish hatcheries.

A COMPARISON OF HINGE-LINE MORPHOGENESIS IN LARVAL SHELLS OF *MYTILUS EDULIS* L. AND *MODIOLUS MODIOLUS* (L.)

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Optical and scanning electron microscopic examination of laboratory reared cultures of larval *Mytilus edulis* (blue mussel) and *Modiolus modiolus* (northern horse mussel) revealed similar hinge-line morphogenesis (straight-hinge stage through metamorphosis) in both species. The hinge apparatus (provinculum) of both mytilids increased in size and complexity throughout larval development, with progressive lateral thickening characteristic of the family Mytilidae. The number of "teeth", while highly variable between individuals with similar shell dimensions, increased significantly with both total shell and provinculum length. Ultrastructural studies of the teeth revealed marked ridged structures which became increasingly apparent with larval growth. In neither species did lateral teeth develop prior to settlement and metamorphosis.

Significant differences at the population level were found between *Mytilus edulis* and *Modiolus modiolus* upon regression and quantitative comparison of each of the following: larval length vs. provinculum length; larval width vs. provinculum length; provinculum length vs. number of teeth; and larval length vs. number of teeth. Such differences should prove useful in discrimination of these two mytilids within the plankton.

CULTURE OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS* (GMELIN) IN NEWFOUNDLAND

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¹ 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.

Techniques used to collect naturally-produced sea scallop (*Placopecten magellanicus*) spat using artificial substrates and their subsequent growth in hanging culture at a near-shore locality in Newfoundland are described.

Of the various substrates employed polyethylene film enclosed in onion bags appeared to be the most suitable. Using this substrate the mean number of live scallop spat collected increased with depth to about 12 m; deeper than this, the numbers settling decreased. Collectors suspended in less than 8 m harboured considerable numbers of starfish. Numbers of live spat and starfish in collecting units were inversely correlated. The mean size (± 1 S.D) of live spat (dorso-ventral axis) at the time of collection was 12.4 ± 0.81 mm with a range of 5.0 to 19.1 mm. There was a slight but significant increase in size with depth, the difference in size being approximately 1.0 mm over the 12 m range sampled.

Growth of scallops in suspended culture was exceptionally good. Preliminary results indicate that shell heights of 12, 24, 36, 48 and 60 month-old animals to be in the order of 36, 66, 80, 95 and 107 mm respectively. Corresponding shell heights of wild scallops from the sea bottom in the same area were x, 27, 46, 66 and 85 mm (x, 12 month-old scallops, were not represented in the study). Mortality is approximately 5% per annum. Animals under two years appear to sustain higher mortalities than those above it.

The relatively sedentary nature of the animal opens up the possibility of resource enhancement of the species through sea ranching the coastal zone. This less expensive but longer route is being examined as well.

ENGINEERING CONSIDERATIONS IN THE DESIGN OF OYSTER DEPURATION PLANTS

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Oyster depuration studies were conducted using four commercial size tanks with varying environmental factors and initial bacterial levels. All four tank designs were suitable for the process,

but two were superior. The primary design features which appear to be important are the residence time of the water and the circulation pattern within the tank. Fecal coliform levels in the water were observed to rise as soon as the oysters were placed in the tank. Depuration occurs more rapidly if the bacteria released by the shellfish are rapidly removed from the tank. The time for a 90% reduction in concentration of dye injected into the tank was found to be roughly twice the theoretical residence time, which is obtained by dividing the total volume by the flow rate.

The residence time may be decreased by increasing the flow of water. An alternative method is to increase the number of oysters held in the tank. Tests showed that depuration was equally successful in identical tanks holding 1.8 and 3 bushels of oysters if the flow of water per bushel of oysters was the same for both tanks.

Good circulation in the tank is needed to prevent dead areas which could become oxygen depleted. Dye tests showed that the residence time was greatly reduced when a water pump was used to increase the flow within the tank. Air lift pumps can accomplish the same result. If the system is properly designed, the resulting current will be smooth and gentle and will not resuspend biodeposits.

OIL AND THE OYSTER IN DELAWARE BAY

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Potentially hazardous effects of petroleum and its derivatives on an economically important population of the American oyster, *Crassostrea virginica*, were investigated to assist development for the Delaware estuary, of more precise water quality standards, compatible for both industry and survival of oyster beds.

Adult and larval oysters were chronically exposed to crude and refined oils adsorbed onto fine kaolin clay. Threshold concentrations for mor-

talities and relative toxicities for different oils were determined.

Adult oysters exposed to 0.3 ppm Nigerian crude showed mortalities twice those of controls. No. 2 fuel oil was approximately twice as toxic as Nigerian crude, which in turn was twice as toxic as Iranian light crude.

Larvae, cultured in natural seawater, developed and metamorphosed in control treatments, but showed increasing mortality, delay in development, and inhibition of metamorphosis at and above concentrations of 0.5 ppm Nigerian crude oil. No. 2 fuel oil was highly toxic to larvae at concentrations as low as 0.25 ppm. Larvae did not show greater sensitivity to oils when compared to adults.

THE ROLE OF *URONEMA*
MARINUM (PROTOZOA)
IN OYSTER HATCHERY PRODUCTION

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In Maine's hatchery production of oysters, significant mortalities at the early juvenile stage have been associated with ciliate protozoan infestations. The predominant ciliate was isolated from live infested oysters in the Spring of 1974 and was identified as *Uronema marinum*. Feeding-type experiments were carried out to determine what food source this ciliate was utilizing in the tank environment. *Uronema marinum* was found to be a bacteriophage and not a histophage; thus, the high mortalities accompanying the early juvenile stage cannot be primarily attributed to the ciliate infestations.

THE USE OF PUMPED RACEWAY SYSTEMS
FOR THE INTERMEDIATE
GROW-OUT OF HATCHERY REARED
BIVALVES

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The survival and growth of hatchery reared bivalves have been investigated in a system of fiberglass raceways through which seawater was continuously pumped. Flow rates of 50 to 60 l/min were maintained in tanks 10 m X 1.3 m with variable depths. The bay scallop, *Argopecten irradians*, was successfully grown in the raceways from a size of 5 mm. Varying raceway depth between 7.5 and 30 cm had no effect on scallop growth. Scallops at stocking densities of 5, 10, 20 and 40 l/raceway and culled back to these densities at bi-weekly intervals grew at rates inversely proportional to population size. Scallops stopped growing when the water temperature declined to 10°C. The surf clam, *Spisula solidissima*, was successfully grown in the system from a starting size of 1 mm. *Spisula* smaller than 20 mm grew equally well in sand and without a substrate. Surf clams larger than 20 mm grew faster in a sand substrate than without and some shell abnormalities were observed in clams grown without substrate. Surf clams exhibited a growth rate inversely proportional to stocking density for biomasses of 1, 4 and 8 l/raceway. The excellent growth rate of these bivalve species in raceways suggests that the use of this system may be a valuable step in the production of shellfish seed.

STATUS REPORT ON THE COMMERCIAL
BLUE CRAB FISHERY
OF THE CAROLINAS AND GEORGIA

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The annual landings, operating unit data, and ex-vessel price for the commercial blue crab (*Callinectes sapidus*) fisheries in North Carolina, South Carolina and Georgia between 1960 and 1976 were analyzed to document recent trends in this fishery and discuss possible factors causing the decline in landings since 1970. Between 1970 and 1976, the total annual landings of blue crabs in the Carolinas and Georgia have declined at an average rate of 2 million pounds per year (1970 landings = 35 million pounds), while 3 thousand traps per year were added to the fishery between 1970 and 1975.

The ex-vessel price for blue crab has increased from \$.05 per pound in 1970 to \$.11 per pound in 1976 with an increase of 20% in the adjusted price per year compared to 1970. This trend suggests a quantity-effect dominant ex-vessel price function. Inaccuracies in the N.M.F.S. reporting system and the lack of recreational and commercial harvesting catch-effort data severely limits the analysis of the current trends. Future trends in the harvesting sector and management research considerations will be discussed.

THE DEVELOPMENT OF THE HINGE LINE IN TROPICAL MUSSEL LARVAE OF THE GENUS *PERNA*

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There is confusion in the literature regarding the synonymy of several species of the genera *Perna* and *Mytilus*. To resolve this problem, I reared larvae of *Perna perna* from Venezuela and *Perna viridis* (= *Mytilus viridis*) from the Philippines through metamorphosis. All living material was quarantined in the laboratory. The results of my scanning electron microscopic examination of these larvae and the larvae of *Mytilus edulis* clearly differentiate hinge line development in the two genera. In both *Perna* species at optimal temperatures and salinities, hinge teeth are well developed

as early as 15 hours after fertilization. Shell length to height ratios decrease as development proceeds with no significant differences between the species. As the larvae approach metamorphosis, the central hinge teeth become more numerous and develop columnar structures. The provinculum broadens laterally in larvae of both genera. Approximately 20 days after fertilization, a series of larger hinge teeth lateral to the central teeth develops in both *P. perna* and *P. viridis* in contrast to larvae of the genus *Mytilus*. Differences in the crystal structure between the lateral and central teeth are apparent. I have examined metamorphosing larvae of the only other member of the genus, *Perna canaliculus* from New Zealand and found similar lateral hinge teeth. The results of my work support the placement of *Mytilus viridis* in the genus *Perna*.

AGE AND MORPHOMETRIC VARIATION IN SUBTIDAL POPULATIONS OF MUSSELS

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The structure of two subtidal syntopic mussel populations (*Mytilus edulis* and *Modiolus modiolus*) was investigated. A total of 703 mussels were collected along two 10-meter transects at depths of 5 and 10 meters off Rutherford Island, Maine. Population densities for *Mytilus* of 50.4/m² and 144.4/m² were recorded at 5 and 10 meters, respectively. Population densities of *Modiolus* were 71.2/m² at 5 meters and 15.2/m² at 10 meters.

A total of 263 *Mytilus* specimens of all sizes were randomly selected and ages accurately determined through examination of annual patterns on acetate peels of sectioned shells. The maximum age (24 years) encountered within the population is considerably greater than that reported to date

within the literature. The age-frequency distribution for the sampled population showed marked cyclic abundance patterns with 49.4% of the population restricted to yearclass multiples of 7. This observed periodicity may be a reflection of a regularly occurring natural event such as a predator-prey oscillation.

Classical modal analysis of size frequency distributions cannot differentiate between annual

recruitment and cyclic abundance patterns with periods greater than 1 year. The potential for frequent interpretive errors by ecologists and paleontologists using modal analysis to infer age structure is discussed.

Modiolus population structure is inferred by comparing crustose coralline incrustation rates for *Mytilus* of known ages with incrustations on *Modiolus*.

NSA PACIFIC COAST SECTION

BREEDING DISEASE RESISTANCE INTO THE
PACIFIC OYSTER

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Since the 1970's, the University of Washington, College of Fisheries has been involved in a cooperative study with the National Marine Fisheries Service and the Washington State Department of Fisheries investigating the causes of Pacific oyster (*Crassostrea gigas*) summer mortalities. Studies have included laboratory testing using elevated water temperatures, nutrient enrichment of sea water, and isolation of implicated bacteria from moribund oysters to simulate summer conditions.

During the past three years, the College of Fisheries has also developed a selective breeding program as an effort toward the prevention of future kills through the introduction of disease resistant stocks. Survivors of laboratory high temperature challenges (above 18 °C) were used as parents to produce potentially resistant F₁ families at the Poulsbo, Washington Sea Farms hatchery during 1974 and 1975. Challenges of these stocks in October, November, and December of 1976 indicated two families to be significantly more resistant to mortality conditions than imported Japanese stocks.

Thirty additional F₁ families were produced during 1976. F₂ families have been produced in 1977 using the 1974 and 1975 F₁ stocks as parents.

Some of these 1975 families have been planted in areas of historic summer mortalities in Washington (Rocky Bay and Mud Bay). Representative stocks of the 1975 F₂ test animals have been given to two hatcheries for large-scale production and testing. Tissues are also being examined electrophoretically for specific genetic information.

OYSTER LARVAE MORTALITY IN
SOUTH PUGET SOUND

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In the summer, particularly late summer, marine waters from many areas of the Puget Sound basin as well as Willapa Bay are found to kill Pacific oyster (*Crassostrea gigas*) embryos and larvae when samples of these waters are brought to the laboratory and used to culture newly-fertilized embryos for 48 hours. Oyster larvae mortality can occur in waters unaffected by point and non-point sources of pollution and is most severe and widely distributed in several inlets in innermost Puget Sound (SPS).

More than 15 years of biomonitoring the marine waters of SPS for acute toxicity to oyster embryos has disclosed the following: larval mortality is a seasonal phenomenon; in Budd and Eld Inlets, appreciable (>20%) mortality commences around June, peaks in late August to early September, and subsides in late October. The scope and severity of the mortality varies greatly between inlets, with Eld Inlet causing the highest average mortality, and Budd, Case, Totten, Carr, and Hammersley Inlets causing lesser mortality, respectively.

Within a particular inlet, mortality increases from the entrance to the head and varies significantly with water depth. Waters 10 to 30 ft in depth usually are more toxic than those at the surface.

The evidence suggests that the toxicity is caused by toxic metabolites of natural planktonic constituents. Although more than one organism is implicated, recent evidence suggests that high densities of the dinoflagellate *Ceratium fusus* can explain a significant percentage of the variation in larval mortality. Removal of most of the *Ceratium* by low pressure—not vacuum—filtration through a 10 μ m screen greatly reduces toxicity.

Work is underway to define the identity of some of the suspected toxic agents and to relate variations in circulation, water quality, and biological productivity between inlets to observed larval mortality.

¹ Research has been supported in part by the Marine Ecosystems Analysis (MESA)-Puget Sound Project of NOAA

HELICOPTER CRABBING

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The newest innovation in crab fishing was off to a flying start off the southern Oregon coast early in 1977 when a helicopter was used to pull oversized crab pots. The helicopter angled with a 6-foot grappling hook on a 25-foot line. The 110-foot double-buoyed pot line was snagged and the 6-foot wide pot was pulled out of the ocean and flown to the landing site. The crabs were removed from the pot and the pot was rebaited and flown back to the fishing site. A loop of line attached to a small hook that was in turn attached to the grappling hook enabled the pilot to release the pot by putting slack in the line after the pot hit the seabed.

Small or female crabs caught in this manner were flown back to the water in a dump container that was lowered to the water where it was tipped over, sliding the crabs out.

Claims by some conventional crab fishermen that small crabs were being "rained across the beach" proved to be grossly exaggerated. Several

days of observation by Department of Fish and Wildlife staff and the State Police showed that the operation damaged very few crabs and was probably less damaging than the boat fishery.

Although only 40 pots were fished, some boat fishermen fear an adverse economic impact on the fishery. The manager of the Oregon All Coast Fishermen's Marketing Association stated publicly that helicopter crabbing is too efficient.

Two helicopter operations made landings in 1977, but it is possible that others may soon become interested.

DISEASE CONTROL IN A MOLLUSCAN SHELLFISH HATCHERY

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The emphasis in shellfish hatchery disease control has been on treatment rather than prevention. This paper presents several operating concepts on disease prevention management employed at International Shellfish Enterprises in Moss Landing, California.

Brood stock must be carefully and frequently selected and histologically monitored to assure the customer that he will receive a disease, parasite and predator free seed product.

Routine sanitation practices through use of isolated culture systems, the careful avoidance of cross-contamination through sterilization of all culture implements, and the routine disinfection of the hatchery water delivery system will help to prevent transfer of disease from one hatchery location to another.

Daily monitoring for the presence of bacterial pathogens is extremely important in order to discover a disease before it becomes unmanageable. Monitoring becomes especially important in screening algal cultures before they are used for feeding.

Antibiotic therapy is used only as a last resort to control disease. When using antibiotics, an effective choice of antibiotic can only be made with the use of antibiotic susceptibility testing, and proper dosages can only be determined through the use of tube dilution sensitivity testing.

Sanitation and bacterial monitoring can contribute significantly to stabilizing shellfish hatchery production output and helps to assure the customer that the product he buys is of the best possible quality and highest survival value.

SQUAXIN ISLAND MANILA CLAM RESEEDING STUDIES

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As a part of a series of studies to determine the future potential for reseeding beaches with small clam seed, Manila clams (*Venerupis japonica*) seed clams were planted at Squaxin Island, (Puget Sound) in May 1976 and have been monitored for growth and recovery. Various protective mechanisms tested in this study have demonstrated differential effects on recovery rates. DuPont Vexar plastic netting, used at different sites, maintained recoveries of 75%, 97%, and 29% after 15 months. Preliminary migration studies have shown that the clams move on the beach after planting; the potential use of this migratory movement to increase the concentration of clam stocks is also being investigated.

OYSTER BREEDING: WHERE CAN IT GO

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Based on the results that have been obtained with other cultured organisms, particularly with agriculturally-raised species, and the genetic variability that has been found in oysters, it should be possible to make significant strides in increasing commercial production of this animal. Before this possibility can be realized a concerted effort must be made, and a systematic program must be designed to initiate the process of domestication. By definition this procedure involves changing an organism for maximum performance under conditions that are amenable to

efficient culture and harvest by man. Present methods of commercial oyster culture employ only part of the domestication process in that, generally a harvestable commodity is grown on the basis on uncontrolled reproduction and semi-controlled growing beds. These methods have some significant implications concerning the interaction of the genetic constitution of the oyster, its environment, and its production potential. These will be discussed with the use of standard genetic models and programs suggested to further enhance the production of oysters utilizing genetic methodology and systematic breeding procedures.

A COMPARISON OF SURVIVAL, GROWTH, AND YIELD OF PACIFIC OYSTERS (*CRASSOSTREA GIGAS*) FROM SEED OBTAINED FROM DIFFERENT SOURCES

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Experimental plantings of the Pacific oyster (*Crassostrea gigas*) were conducted over a 3-year period with the objective of establishing the relative quality of various sources of oyster seed and to develop methods to improve survival and growth, especially during the first growing season. The results were mixed, depending on the area where grown and the methods used; but using conventional cultural practices, it appears that Japanese oyster seed will generally produce higher yields compared to equivalent groups of hatchery-produced or wild domestic seed. Japanese seed, however, may suffer higher mortality during the second year in some locations, indicating resistance to mortality for domestic oysters. The variables of seed size, seed density, hardening methods, and off-bottom rearing were evaluated. The initial size of the seed was found to be important in some cases, but the problems of small size were often more than offset by increased numbers of spat per shell. Density-dependent mortality was found to be linear through the range of densities studied. Studies also showed that some alternative methods of seed handling could improve the

ultimate yield. In particular, it was found that off-bottom rearing for the first growing season more than doubled the production by the end of the second season. The improvement was especially apparent for the domestic seed. Some of the "conventional wisdom" regarding the relative quality of seed and the factors that determine quality were found not to be generally true, and it was apparent that each oyster grower must determine the factors that are most important for his particular cultural situation.

PRELIMINARY REPORT ON MANILA CLAM
RESEEDING PROGRAM AT FIVE PUGET
SOUND BEACHES

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Receiving support from the Washington State Sea Grant Program, the College of Fisheries along with the Washington Departments of Fisheries and Natural Resources have continued to investigate the feasibility of planting hatchery spawned Manila seed clams on Puget Sound beaches. During the past 1½ years the major emphasis of the project has been centered on determining the causes for low recoveries of planted clams. Studies carried out to gain a better understanding of the problems involved have included providing protection for planted clams, planting clams in modified substrate, determining clam predators and testing for movement of planted clams. The rearing of small seed clams in suspended sand-filled trays has also been conducted for the purpose of obtaining advanced size clam seed for subsequent grow out on the beach. While the economics of clam reseeding do not yet favor commercial application, there seems to be a potential for this which may be realized by further research.

SEED OYSTER PRODUCTION IN THE
SALTON SEA CALIFORNIA

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The Salton Sea is an inland body of salt water located in the southern California counties of Riverside and Imperial. The sea is approximately 70 kilometers long and 25 kilometers wide with the water surface about 65 meters below sea level. The salinity currently ranges from 33 0/00 to 37 0/00. The ionic content of Salton Sea water is not the same as that found in oceanic water as the salt comes from concentrated irrigation waste water. Water temperatures, taken three meters below the surface, range from winter low of 10°C to a summer high of 37°C.

Attempts in the 1950's to establish oysters in the Salton Sea were unsuccessful. Adult pacific oysters, *Crassostrea gigas*, will live about 30 days in Salton Sea water. It appears that even though the Salton Sea water has abundant plankton the water anesthetizes ciliary action and adult oysters are unable to feed. Experiments utilizing Salton Sea water to spawn oysters and culture larvae have shown that all stages survive well and a commercial spat fall can be obtained. Adequate spawning and culture temperatures are present from May through November each year. During this period naturally occurring phytoplankton counts range from 0.5 to 3 million cells/liter.

Plans for a commercial oyster hatchery at the Salton Sea have been reviewed and modified by local, state, and federal regulatory agencies and all necessary permits have been granted. Sufficient financial support has been obtained to begin construction, and it is planned that the facility will set its first commercial oyster larvae during the late spring of 1978.

PRELIMINARY STUDIES ON THE
DEVELOPMENT
OF A SYNTHESIZED DIET FOR JUVENILE
OYSTERS, *CRASSOSTREA GIGAS*

M.A. Toner

The growth of juvenile Pacific oysters fed equal amounts (based on ash free dry weights) of algae (*Pseudoisochrysis paradoxa*), lysed algae, dried oyster meat and encapsulated lysed algae was monitored in three experiments. Dried oyster meat and encapsulated lysed algae were also fed as supplements to lysed algae at three levels: 25, 50 and 75 percent of the total ash free dry weight of the diet. The growth of oysters fed lysed and whole algal cells with and without the addition of sodium sulfamethazine (Sulmet®) was also compared. Growth was measured as the difference in ash free dry meat weight between treatments and an initial sample frozen at the beginning of the experiment.

In the first experiment, oysters fed algae alone showed an increase in ash free dry weight that was significantly greater than that of oysters fed dried oyster meat alone and as a supplement to algae. In the second experiment, oysters fed lysed algae treated with or without Sulmet® showed a significant decrease in ash free dry weight from the initial sample. Oysters fed algae with and without treatment with Sulmet® did not show a significant increase in ash free dry weight. In the third experiment, oysters fed starch encapsulated algae and algae with and without supplementation with encapsulated algae increased significantly in ash free dry weight as compared to the initial sample.

Encapsulation appears to be a process which could be used as a delivery system for feeding synthesized diets to juvenile oysters.

CLAM RESOURCE MEASUREMENT FOR ESTIMATION OF POLLUTION DAMAGE¹

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Commonly used statistical procedures are geared to assure we do not state in error that a clam population has diminished in face of pollution while little attention has been given to the corollary need by private and public resource managers to have assurance that a given reduction in the clam resource will be detected. This paper deals with the sampling requirements for detection

of change in population abundance of native little neck clams (*Protothaca staminea*) on specific plots in the north Puget Sound region. Example data are presented which indicate that from 75 to 20,000 samples are required for detection of a 40 percent to 5 percent change in abundance on sample plots respectively. A pre-mapping procedure of sample stratification which effectively reduced the sampling requirement by one-half is also discussed.

¹ This paper is based on work performed under U.S. Energy Research and Development Administration Contract EY-76-C-06-1830

MUSSELING IN ON A NEW MARKET

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The Mussel Project is currently involved in 3 areas of study: mussel set prediction; hatchery development; and market investigation. Monitoring of plankton and spat collectors has revealed no significant mussel sets for spring and summer 1977 at study sites in Seabeck and Clam bays. Plankton and water quality factors of temperature, salinity, and phytoplankton abundance will continue to be monitored to provide a historical baseline for the study sites.

The investigation of hatchery techniques for rearing and setting mussel larvae has been undertaken to provide information on the larval development and settlement of local mussel stocks and to develop a commercially feasible hatchery system. The use of larval dimensions for identification of planktonic mussel larvae has been strengthened by information gained from the hatchery revealing that dimensions of larvae obtained from Puget Sound stocks of *Mytilus edulis* are comparable to those from New England stocks.

Recent newspaper and magazine articles coupled with the publishing of a mussel cookbook have increased public awareness of the delights to be found in mussel dishes. A recent survey of 300 restaurants in Washington State reveals a significant interest in mussels by restaurant owners and

identifies poor consumer awareness, inadequate supply and product quality to be the major impediments for development of this market. Examination of mussels offered in retail markets reveals that a poor product quality may be a great detriment to the advancement of mussels as a household food item.

PIGEON POINT SHELLFISH HATCHERY: PAST, PRESENT AND FUTURE

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The Pigeon Point facility was established in 1965 as a shellfish hatchery for the mass culture of bivalve molluscs from egg to seed-sized juvenile stages. Cultchless seed was developed at Pigeon Point in 1968. Commercial success attained from this development stimulated further expansion in 1970 in which a new building was built at Pigeon Point and a cultch-setting facility was established in Moss Landing.

The expansion brought about serious production problems: larval mortality and inability to grow sufficient algae to feed the spat. During this period the Pacific Northwest seed market was penetrated, but the inability to produce quality seed quickly resulted in marketing failures.

The production failures became increasingly severe and in 1974 the operation went into a well-financed research and development mode resulting in a successful pilot production program two years later.

In January, 1976, a highly favorable technical evaluation was made of the facility by an outside group of mariculture scientists from such institutions as Scripps, Woodshole, U.C., and O.C.U. The group also included individuals from commercial mariculture businesses.

On the basis of this evaluation, the facility was redesigned and successfully put into commercial operation in November, 1976.

Today, Pigeon Point Shellfish Hatchery is again producing high quality cultchless oyster seed at a yearly rate of about 30 million seed. A wide variety of species and sizes ranging from 2-3 mm and 25-40 mm (1 to 1.5 inches) are available.

While growers in Oregon have had a great deal of success with the seed, the majority of the product is planted in Europe and the Eastern United States.

In the future, Pigeon Point intends to increase production levels significantly and add new species to the inventory list. We hope that more growers in the Pacific Northwest will try our large cultchless seed in their growouts. We would greatly appreciate suggestions of how we might be able to fit into the oyster industry in this region. Samples of our products are available at limited cost.

VIBRIO ANGUILLARUM AND LARVAL MORTALITY IN A CALIFORNIA COASTAL SHELLFISH HATCHERY

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The Pigeon Point Shellfish Hatchery has had a mixed history of success in developing profitable oyster spat production primarily because of larval mass mortalities due to unknown causes. The predominant bacterial species recently isolated from moribund oyster veliger larvae produced under hatchery conditions was identified as *Vibrio anguillarum*. Infection of healthy larvae, and repeated recoveries of this bacterium from diseased larvae confirmed this bacterial species to be one cause of serious epizootics within the hatchery. Routine screening for this organism and observation of larval behavior, coupled with appropriate hatchery design and management techniques have controlled this cause of larval mortality.

In the paper "Mercenaria culture using stone aggregate for predator protection" by Castagna and Kraeuter, Vol. 67, 1977, there is an error in the last sentence before the results. The sentence states, "Once the area had been stabilized, small clams were broadcast over the aggregate at an average density of approximately 31/sq. m." It should have read 3100/sq. m.

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