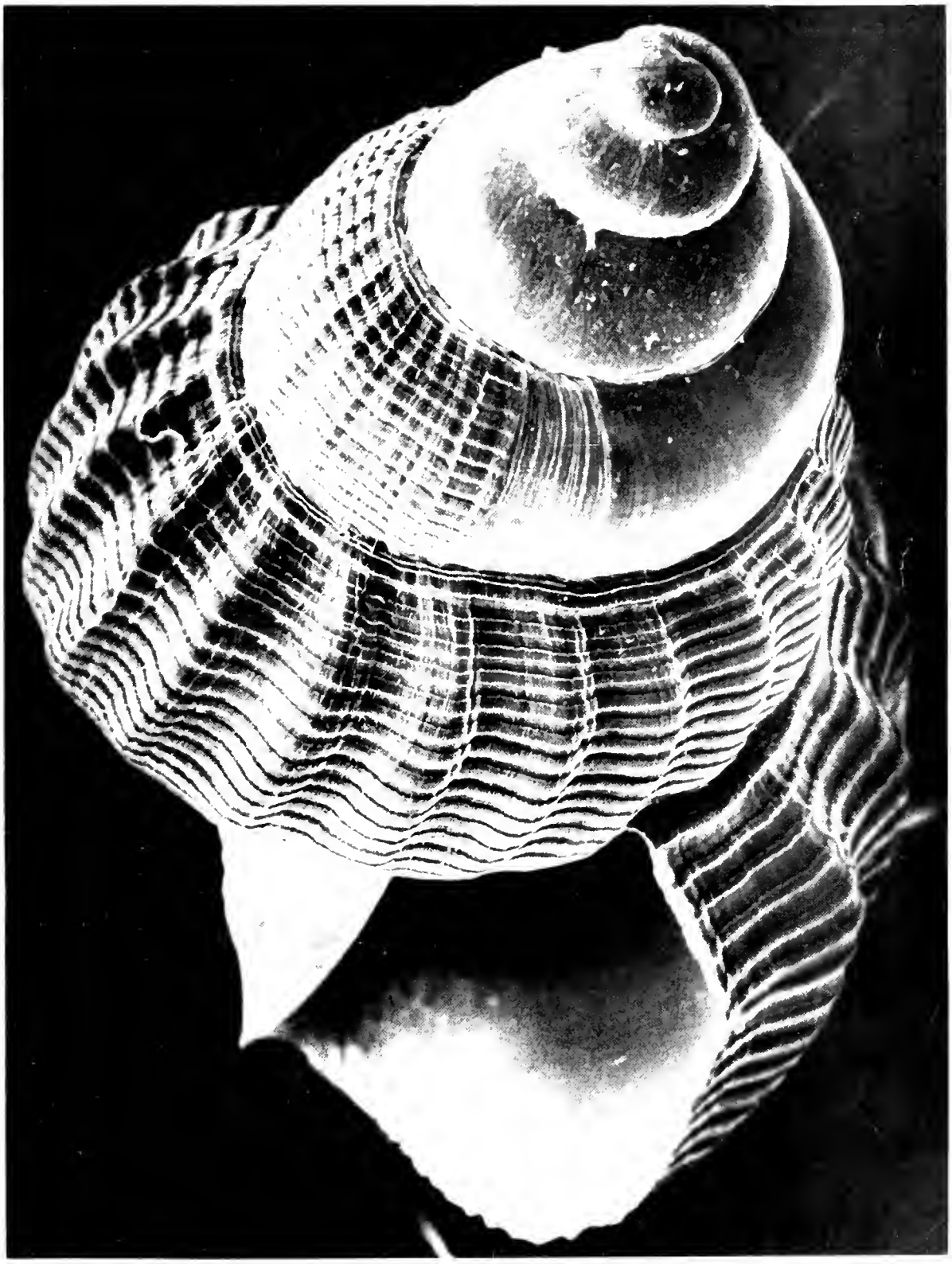
JOURNAL OF SHELLFISH RESEARCH

VOLUME 4, NUMBER 1 JUNE 1984



The *Journal of Shellfish Research* (formerly *Proceedings of the National Shellfisheries Association*) is the official publication of the National Shellfisheries Association

Journal of Shellfish Research
Volume 4, Number 1
ISSN: 00775711
June 1984

Journal of Shellfish Research, Vol. 4, No. 1, 1–3, 1984.

SYNOPSIS OF RECENT RESEARCH ON THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ

SCOTT E. SIDDALL
Marine Sciences Research Center
State University of New York
Stony Brook, New York 11794

The queen conch *Strombus gigas* Linné is much more than an important marine resource of shallow tropical water from Florida and Bermuda to the Lesser Antilles and Central America. It is an economic and cultural symbol of the region. The queen conch appears on postage stamps, coins and currency of several Caribbean nations; huge statues of the conch are not uncommon in town plazas. Nearly every language or dialect in the Caribbean has a specific term for *S. gigas,* from caracol in Mexico, cobo in Cuba, carco in the Netherlands Antilles, to lambis in the French West Indies. For centuries, the species has derived its socio-economic importance from the subsistence, or artisanal, fisheries it has supported. The conch's slow movement and accessibility in shallow waters made it an ideal, high-protein staple in the diets of many Caribbean islanders. In the past, a kilogram of cleaned meat could be gathered in minutes from half a dozen or so large adults taken in 1 m deep water. Live conchs can be kept underwater alive and fresh for days even without refrigeration when strung on rope through holes cut into the flared lip of the shell.

In the mid-1970's, the outlook for these subsistence fisheries for conch began to change. According to Stevely and Warner (1978) and Dubois (1985), demand for conch meat in the United States increased dramatically because of new restrictions on catches in Florida, and from increased demand from both tourists and immigrating Latin and West Indian populations in southern Florida. Imports of conch meat through Miami, FL, rose from 214,000 kg in 1970 to more than 700,000 kg in 1981 (Brownell and Stevely 1981). Biological overfishing of many populations of queen conchs became apparent and several nations, notably Belize and the Turks and Caicos, developed fishery management plans to save dwindling stocks.

The conflict between commercial fisheries for profit and traditional, subsistence fisheries for food became more apparent as did the need for management and research; yet, despite the nutritional and social significance to subsistence fisheries (Dubois 1985), it is difficult to imagine a unified, regional management plan for a fishery resource such as the queen conch which is distributed across more than 21 political jurisdictions. It is even more difficult to coordinate support for research on an important subsistence resource with an aggregate **commercial** value of less than $5 million (US) per year.

During the early 1980's, however, three significant research efforts were launched which set the tone for much of the research and development efforts that have followed. In Feburary 1980, the Wallace Groves Aquaculture Foundation of Freeport, Bahamas, funded a study at the University of Miami on hatchery production and growout of queen conchs for purposes of replenishing depleted natural stocks. In January 1981, the National Marine Fisheries Service and the Office of Sea Grant sponsored a research program at the University of Puerto Rico with similar goals. The Foundation for PRIDE, a not-for-profit organization working in the Turks and Caicos islands, stepped up efforts to culture queen conch larvae based on several years experience with the local fishery and conch stocks.

Prior to 1976, much of the scientific literature on *Strombus gigas* dealt with the taxonomy, distribution, and general ecology of the animal (see the excellent bibliography by Darcy 1981). Very few papers even acknowledged the socio-economic role of the species in the Caribbean. Notable exceptions were the larval culture studies of Willard Brownell (1977) at Islas de Los Roques, Venezuela, and the paper by Carl Berg (1976) on the practicality of commercial culture of the species.

Over the past five years, a number of research advances have come to the fore, particularly in areas of fisheries management, population ecology, and basic biology of the species. Several conch fisheries have been described (Nardi 1982, Gibson et al. 1983, DuBois 1985). The spatial and temporal variabilities of growth and survival have been documented (e.g., the studies of Weil and Laughlin 1985, Wood and Olsen 1983) and generalized models of mortality have been described (Appeldoorn 1985). Laboratory studies of predation have been reported (Jory and Iversen 1983). Possibilities for inducing copulatory behavior for egg production have been explored (methods of Ram et al. 1982, applied by C. J. Berg, Marine Biological Laboratory, Woods Hole, MA [unpublished results], and briefly noted by Siddall 1983). Davis et al. (1984) reported on breeding behavior of captive populations of queen conchs. Genetic analyses of differentiated stocks of queen conchs continue (C. J. Berg, Marine Biological Laboratory, Woods Hole, MA, and USAID Conch program, Belize, Central America) and genetic evidence of multiple mating has been found (Steiner and

Siddall, unpublished results). Feeding relationships of larvae (Pillsbury 1984, 1985; Siddall 1983) and juveniles (Creswell 1984a, b) have been investigated. Respiratory physiology of developing conch larvae has been detailed by Erickson (1984, 1985). Mianmanus (1984) has examined responses of conch larvae to red macroalgae which have been implicated as substrates for settlement and metamorphosis. Sanders (1984) has documented the toxicity of copper ions to juvenile conchs.

Generally, the goals of all of these research efforts have been to gather information needed either for the management of exploited conch stocks or the replenishment of depleted populations. DuBois (1985) summarized the opportunities and constraints for conch fisheries management and recommended extended collection of catch-and-effort data, improved educational programs, and fisheries management plans with practical objectives. The culture of queen conch juveniles for extensive replenishment programs, or of adults for market sale, still figures prominently in current research programs. In spite of the clear fact that research activity has increased dramatically since 1980, there are no outstanding examples of successful fisheries management or population replenishment through aquaculture. Many more years of effort may be required before tangible benefits to the fisheries accrue from research. Fortunately, the research effort continues.

At least eight research and development programs are active in 1985. These include the Foundation for PRIDE (Provodenciales, Turks and Caicos Islands), the Department of Marine Sciences of the University of Puerto Rico, the Mexican government's Centro de Aquacultura in Quintana Roo, two U.S. Agency for International Development programs in Belize and Haiti, a new facility in Martinique operated by the French fisheries development organization (IFREMER), the Institute for Applied Research in the U.S. Florida Keys, and Bonaire's Carco Project.

Those of us working within these research programs have been fortunate to have a continuing series of scientific fora for presentation and review of our work. In 1981, The Groves Foundation sponsored a workshop on queen conch fisheries and mariculture through which many of these widely separated research groups coordinated their efforts. A conch fisheries management and mariculture session was held during the 35th meeting of the Gulf and Caribbean Fisheries Institute in November 1982. Another workshop on fisheries management of the queen conch was held at the Gulf and Caribbean Fisheries Institute meeting convened in Martinique, French West Indies, in November 1985.

Where other symposia and workshops have concentrated on fisheries management and aquaculture, the theme of this issue of the *Journal of Shellfish Research* focuses on the basic biology of the queen conch. The following contributions represent many of the papers presented at the "Special Symposium on the Biology of the Queen Conch *Strombus gigas*" held during the National Shellfisheries Association's meeting in June 1983, at Hilton Head, South Carolina.

REFERENCES CITED

Appeldoorn, R. S. 1985. Changes in the rate of natural mortality over the life history of the queen conch *Strombus gigas*. Program paper and abstract, 77th Annual Meeting of the National Shellfisheries Association, June 1985. *J. Shellfish Res.* 5(1): in press.

Berg, C. J. 1976. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. *Mar. Biol. (Berl.)* 34:191–199.

Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and *S. pugilus* in Los Roques, Venezuela. *Bull. Mar. Sci.* 27:668–680.

_____ & J. M. Stevely. 1981. The biology, fisheries, and management of the queen conch, *Strombus gigas*. *U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 43(7):1–12.

Creswell, R. L. 1984a. Ingestion, assimilation and growth of juvenile queen conchs, *Strombus gigas*, fed experimental diets. Miami, FL: Univ. of Miami. 107 p. Master's Thesis.

_____ . 1984b. Ingestion, assimilation and growth of juveniles of the queen conch *Strombus gigas* Linné fed experimental diets. *J. Shellfish Res.* 4(1):23–30.

Darcy, G. H. 1981. Annotated bibliography of the conch genus *Strombus* (Gastropoda, Strombidae) in the Western Atlantic Ocean. *U.S. Natl. Oceanic Atmos. Admin. Tech. Rep.* NMFS–SSRF–748:16 p.

Davis, M., B. A. Mitchell & J. Brown. 1984. Breeding behavior of the queen conch *Strombus gigas* Linné held in a natural enclosed habitat. *J. Shellfish Res.* 4(1):17–21.

DuBois, R. 1985. Coastal fisheries management; lessons learned from the Caribbean. Clark, J. ed. *Coastal Resources Management: Development Case Studies.* Renewable Resources Information Series (U.S. Natl. Park Serv. and U.S. Agency Internatl. Develop.). Coastal Publ. No. 3:292–370. Available from: Research Planning Institute, Inc., Columbia, SC.

Erickson, J. T. 1984. Open-gradient-diver respirometry applied to free-swimming larvae of the queen conch *Strombus gigas* Linné. *J. Shellfish Res.* 4(1):5–15.

_____ . 1985. Age-specific respiration of larval queen conch, *Strombus gigas* Linnaeus using open gradient diver microrespirometry. Miami, FL: Univ. of Miami. 79 p. Master's Thesis.

Gibson, J., S. Strasdine & K. Gonzales. 1983. The status of the conch industry of Belize. *Proc. Gulf Caribb. Fish. Inst.* 35:99–107.

Jory, D. E. & E. S. Iversen. 1983. Queen conch predators; not a roadblock to mariculture. *Proc. Gulf Caribb. Fish. Inst.* 35:108–111.

Mianmanus, R. 1984. Metamorphosis of *Strombus gigas* Linné and *Aplysia brasiliana* Rang in laboratory culture. *J. Shellfish Res.* 4(1): 95 (Abstract).

Nardi, G. C. 1982. An analysis of the queen conch fishery of the Turks and Caicos Islands, with a review of a new, multi-purpose dock receipt. Stony Brook, NY: State Univ. of New York. 47 p. Master's Thesis.

Pillsbury, K. S., 1984. Nutrition of *Strombus gigas*, queen conch larvae. Miami, FL: Univ. of Miami. 145 p. Master's Thesis.

_____ . 1985. The relative food value and biochemical composition of five phytoplankton diets for queen conch, *Strombus gigas* (Linné) larvae. *J. Exp. Mar. Biol. Ecol.* 90:221–231.

Ram, J. L., M. L. Ram & J. P. Davis. 1982. Hormonal control of

reproduction in *Busycon:* II. Laying of egg-containing capsules caused by nervous system extracts and further characterization of the substance causing egg capsule laying. *Biol. Bull. (Woods Hole)* 162:360-370.

Sanders, I. 1984. Sublethal effects of copper on juveniles of *Strombus gigas* Linné. *J. Shellfish Res.* 4(1):31–35.

Siddall, S. E. 1983. Biological and economic outlook for hatchery production of juvenile queen conch. *Proc. Gulf Caribb. Fish. Inst.* 35:46–52.

Stevely, J. M. & R. E. Warner. 1978. The biology and utilization of the queen conch *Strombus gigas* L., in the Florida Keys and throughout its geographical range. Report to the Florida Cooperative Extension Service, Palmetto, FL.

Weil, E. & R. Laughlin. 1984. The biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linné in the Archipelago de Los Roques National Park. *J. Shellfish Res.* 4(1):45–62.

Wood, R. S. & D. A. Olsen. 1983. Application of biological knowledge to the management of the Virgin Islands conch fishery. *Proc. Gulf Caribb. Fish. Inst.* 35:112–121.

Journal of Shellfish Research, Vol. 4, No. 1, 5–15, 1984.

GRADIENT–DIVER RESPIROMETRY APPLIED TO FREE–SWIMMING LARVAE OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ

JEFFERY T. ERICKSON[1]
Rosenstiel School of Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149

ABSTRACT Open gradient-diver microrespirometry as applied to free-swimming veliger larvae is described in detail. The gradient diver consists of a small ampulla of capillary glass tubing, closed at one end and drawn out into a narrow tail at the other, open end. A small gas space separates the larva in the closed end from a CO_2-absorbing alkali solution filling the tail of the diver. The entire unit is placed in a linear sodium sulfate gradient. As the animal respires, the compound density of the diver increases due to oxygen consumption and the absorption of CO_2 from the gas space. Measurement of the sinking rate of the diver through a known gradient allows the oxygen consumption of the enclosed animal to be evaluated. Oxygen-uptake rates determined with this method for 4-, 7-, 10-, and 13-day-old queen conch veligers are presented. The advantages and disadvantages of the technique are discussed.

KEY WORDS: gradient-diver respirometry, *Strombus gigas*, queen conch larvae

INTRODUCTION

The Cartesian diver gasometer, introduced by Linderstrom-Lang (1937, 1943) and developed by Holter (1943, 1961), Zajicek and Zeuthen (1961), and Holter and Zeuthen (1966), is an extremely sensitive instrument capable of accurately detecting minute changes in gas volume. It has been successfully used in biochemical studies (Boell and Shen 1950, Zajicek and Zeuthen 1961, Hamburger et al. 1977) and respiration studies involving eggs and small individual marine and terrestrial organisms (Zeuthen 1947, 1949, 1953; Webb 1969; Zeuthen and Hamburger 1972; Luxton 1975; Steigen and Klekoswki 1977). The technique requires constant attention, a considerable amount of specialized equipment, and a high degree of skill in manufacturing and manipulating the divers.

Gradient-diver respirometry was first developed by Lovlie and Zeuthen (1962) in response to these inherent difficulties and inconveniences. Theoretical considerations for a closed gradient-diver respirometer may be found in that paper. Modifications by Nexo et al. (1972) simplified the technique further, allowing direct gradient calibration and operation of the divers under atmospheric pressure. Although based on a different principle than the Cartesian diver, gradient-diver respirometry retains a respectably high degree of sensitivity and precision.

The basic unit of the respirometer is the ampulla diver, a small piece of capillary tubing, closed at one end and drawn out into a narrow tail at the other, open end. A small gas space separates the experimental animal in the closed end from a CO_2-absorbing alkali solution in the tail of the diver. A control diver contains no animal, but has similar dimensions to the experimental diver.

Divers are placed in a linear sodium sulfate gradient. Initially, the divers float in quasi-equilibrium in the upper portion of the gradient, diver buoyancy equalling the weight of the displaced gradient fluid. As the animal respires, oxygen is consumed and CO_2 is absorbed from the gas space within the diver. As this volume decreases, gradient fluid is drawn up into the tail of the diver, and the compound density of the diver increases. As a result, the diver slowly sinks, remaining in quasi-equilibrium with the increasing density of the gradient. Measurement of the sinking rate of the diver through a known gradient (calibrated with a series of small density standards) allows the oxygen consumption of the enclosed animal to be evaluated.

The control diver responds to changes in atmospheric pressure and temperature; in effect, it acts as a "thermobarometer" (Nexo et al. 1972). If the size and shape of the control diver are similar to that of the experimental diver, the migration of the control may be used to compensate for the migration of the experimental due to these factors.

The following equations from Nexo et al. (1972) are used to calculate the oxygen consumption of the experimental animal. They assume a linear gradient, a similarity between control and experimental divers, and the condition that the experimental diver migrates downward in the gradient (another equation is used if the diver moves upward in the gradient due to gas evolution):

$$\Delta V_{NTP}\ (\mu l) = K_V\ (\Delta H - \Delta H_c) \qquad (1)$$

$$K_V\ (\mu \ell \cdot mm^{-1}) = (273/10300T)\ [(P_o \cdot U/\phi_o) \cdot (d\phi/dH) - V_o \cdot \phi_o] \qquad (2)$$

[1]Present address: Department of Physiology, School of Medicine, University of North Carolina, Chapel Hill, NC 27514.

where:

ΔV_{NTP} = gas volume change (oxygen consumption) at standard temperature and pressure ($\mu\ell$),
K_v = "volume diver constant" for downward migration of the diver ($\mu\ell \cdot mm^{-1}$),
ΔH = downward migration of the experimental diver (mm),
ΔH_c = migration of the control diver (mm),
273/10300 T = conversion factor to standard temperature and pressure,
T = absolute temperature (°K),
P_o = initial pressure of gases inside the diver at the beginning of the experiment (mm H_2O; mm H_2O = mm Hg · [10300/760]),
U = total volume of the diver ($\mu\ell$),
ϕ_o = density of the gradient at the initial position of the aperture of the diver (mg · $\mu\ell^{-1}$),
$d\phi/dH$ = gradient slope (mg · $\mu\ell^{-1}$ · mm^{-1}), and
V_o = initial gas volume of the diver at the beginning of the experiment ($\mu\ell$).

The parameters of the "volume diver constant" may be defined as follows:

$$P_o \text{ (mm } H_2O) = B + \tfrac{1}{2}(\phi_o + \phi_{surf})(H_{surf} - H_o) - \pi \quad (3)$$

where:

B = barometric pressure (mm H_2O),
$\frac{1}{2}(\phi_o + \phi_{surf})$
$(H_{surf} - H_o)$ = hydrostatic pressure (mm H_2O),
ϕ_{surf} = density of the gradient at the surface (mg · $\mu\ell^{-1}$),
H_{surf} = relative position of the gradient surface (mm),
H_o = relative position of the aperture of the diver (mm), and
π = water vapor pressure at temperature T inside the diver (mm H_2O);

and:

$$U(\mu\ell) = (m_{gl}/\phi_{gl}) + [(m_f - m_{gl})/\phi_{H_2O}] \quad (4)$$

where:

m_{gl} = weight of the empty diver (mg),
m_f = weight of the diver filled with distilled water (mg),
ϕ_{gl} = density of the glass of the diver (2.23 mg · $\mu\ell^{-1}$), and
ϕ_{H_2O} = density of distilled water (1.00 mg · $\mu\ell^{-1}$);

and:

$$V_o(\mu\ell) = m_{gl}([1/\phi_{om}] \quad [1/\phi_{gl}]) \quad (5)$$

where:

ϕ_{om} = density of the gradient at the level of the lower meniscus inside the diver at the beginning of the experiment. This roughly corresponds to the volume center of the diver.

Moller and Ottolenghi (1964), Nexo et al. (1972), Hamburger (1981), and Petersen (1981) described the basic techniques essential to gradient-diver respirometry. None of these authors, however, presented a complete description of the entire method and all omitted mentioning techniques that would make gradient-diver respirometry easier to use. The primary goal of this paper is to present a comprehensive description of open gradient-diver methodology, particularly as modified for use with free-swimming veliger larvae. These modifications of equipment and technique are suitable in most situations where gradient-diver respirometry is applicable. I hope that this addition to the literature will encourage the use of a neglected micro-respirometric technique, the potential of which has not been fully explored.

MATERIALS AND METHODS

Manufacture of Density Standards

The procedures of Moller and Ottolenghi (1964) were followed with some modifications. Precision-bore, thin-walled capillary tubing (inner diameter 0.5 mm; inner: outer diameter ratio = 0.86) was specially made (Friedrich and Dimmock, Inc., Millville, NJ). These dimensions resulted in final standards with a suitable weight-to-volume ratio.

A convenient length of tubing was sealed at one end with a microtorch (Model No. 23-1001-A, Wale Apparatus Company, Hellertown, PA). Using a fine-tip forcep, a small bead precursor was pulled off in the flame (Figure 1, A–C). The precursor was 1 to 2 mm in length, hollow, and sealed at both ends with little excess glass. The precursors were transferred (10 to 15 at a time) to an asbestos pad and a hot flame from the microtorch was played upon each precursor from directly above. During heating, the glass melted, the air inside expanded, and the precursor rounded out into a hollow glass sphere (Figure 1, D–F). Only hollow glass spheres within the anticipated density range (1.00 to 1.10) were chosen as density standards. Transferring and handling of individual beads and bead precursors were easily accomplished with the tip of a small watercolor paintbrush.

Calibration of Density Standards

Preliminary Classification Density standards covering a density range of about 1.00 to 1.10 were required. All beads were placed in a quantity of distilled water. Those

that floated were too light and were discarded. The remaining beads were then placed in a volume of chlorobenzene (density, 1.106). Those that sank were too heavy and were discarded. The remaining beads covered the density range of 1.00 to 1.106. These beads were separated into preliminary density categories:

1. All beads were placed in a measured volume of chlorobenzene, in which they floated. Measured small amounts of toluene (density, 0.86) were added with mixing until a number of beads sank to the bottom of the test tube.
2. The "sinkers" and "floaters" were separated and allowed to dry. Those that sank were put into a container labelled with the chlorobenzene:toluene ratio in which they sank.
3. The beads that remained floating were transferred to another test tube containing the original volume of chlorobenzene. Slightly more toluene than in the first separation was added, with mixing, until another number of beads sank. Sinkers and floaters were separated, as before, with proper labelling.
4. This procedure was continued until all beads had been separated into a number of preliminary density categories covering the original density range.
5. Each group of beads was examined under a dissecting scope and those conforming most closely to a spherical shape were retained.
6. Spherical density standards were placed within a gradient of the anticipated density range (see ***Production of Linear Density Gradients***) and allowed to reach equilibrium positions. Beads located at equally spaced intervals over the middle portion of the anticipated density gradient were chosen for final calibration.

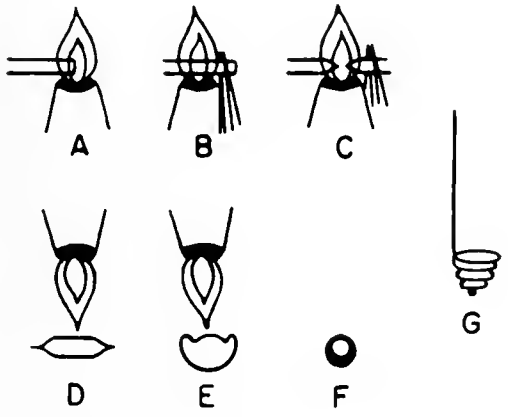


Figure 1. Manufacture of density standards. (A) One end of the capillary tube is sealed; (B–C) The capillary is heated and a bead precursor is pulled off; (D–E) The bead precursor is rounded out by heating from directly above into (F) a finished density standard. (G) Implement for removal of density standards from gradient (adapted from Moller and Ottolenghi [1964], Figures 2, 3, and 7).

Final Calibration Final calibration of individual density standards was carried out at 25°C ± 0.05°C. A 1 ℓ inner water bath (stirred) was surrounded by a 5-ℓ, insulated outer water bath. The outer bath was connected to a suitable constant temperature water bath and circulator (Forma Model No. 2160, Forma Scientific, Marietta, OH) via two insulated polyethylene leads (Figure 2).

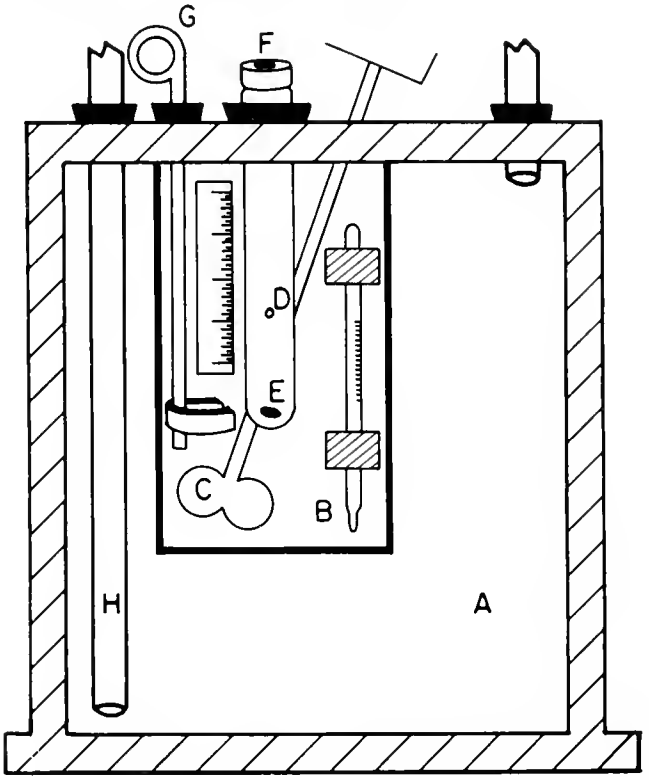


Figure 2. Outer and inner water bath assemblies for calibrating density standards: (A) outer water bath; (B) inner water bath; (C) stirrer; (D) density standard; (E) "flea" stirrer; (F) gas chromatograph septum; (G) magnet pull rod; (H) water circulator inlet.

A single bead was placed in a 10-mℓ test-tube mixing chamber, with a stirring bar and the preliminary category ratio of chlorobenzene:toluene for that bead. The top of the mixing chamber was screwed down tightly, sealing a gas chromatograph septum between the cap and the test tube. The mixture was thoroughly stirred, placed in the inner water bath and allowed to equilibrate for 10 to 15 min. After equilibrating, one or the other of the pure organic solvents was added dropwise with adequate mixing (magnet) until the bead floated neutrally buoyant in the mixture. The solvents were added to the mixing chamber by injection with a microliter syringe through the gas chromatograph septum. Care was taken to ensure that the solvent dropped directly into the liquid and did not contact the sides of the test tube above liquid level. A needle head was inserted through the septum to alleviate pressure buildup within the mixing chamber.

The behavior of the bead was observed for at least 15 min. If the bead neither sank nor rose a vertical distance of 4 mm (using a scale affixed to the inner water bath), the bead was defined as having the same "density" as the liquid in which it was suspended.

After obtaining neutral buoyancy, the mixing chamber was tightly capped to prevent evaporation of either component from the solvent mixture. The density of each mixture (at 25°C ± 0.01°C) was determined with a Sodev Model No. 02D vibrating flow densimeter with an accuracy of at least 1×10^{-4} g · mℓ$^{-1}$. Because, at neutral buoyancy, the density of the fluid equalled the specific gravity of the bead, the "density" of the bead was known. It is important that the density determinations are carried out at the same temperature at which the standards are calibrated. Ideally, actual experiments using these standards should be run at this temperature as well. Also, density standards should be stored individually in labelled vials and great care taken in handling them during experimental procedures.

Production of Linear Density Gradients

Linear sodium sulfate gradients were produced according to Nexo et al. (1972) with some modifications. Two similar 250-mℓ glass beakers, fitted with 10-mm inner-diameter outlets, were connected by a soft rubber tube (Figure 3). The flow through this tube was controlled by a pinchcock. After closing this connection, about 125 mℓ of distilled water were added to beaker B and a similar amount of an aqueous solution of sodium sulfate (density, 1.09 g · mℓ$^{-1}$) was added to beaker A. The sodium sulfate solution was constantly mixed with a magnetic stirrer and the entire system was mounted above a 250-mℓ graduated cylinder immersed in a water bath that was temperature controlled to 25°C ± 0.5°C. A soft rubber tube (also controlled by a pinchcock) connected a 6.5-mm outlet at the base of beaker A to a Pasteur pipette, the free end of which was specifically drawn out into a fine tip (opening, 0.5 mm). The pipette was placed through a hole in the side of the graduated cylinder such that the tip rested against the opposite inner wall of the cylinder.

After purging the rubber tubing of air bubbles and initiating stirring, the density gradient was produced over 2 to 2.5 hr by releasing the pinchcocks simultaneously and allowing a slow drift of progressively more dilute salt solution down the inside of the graduated cylinder. This flow layered out to form a density gradient over a vertical distance of about 240 mm. Care was taken to prevent backflow between beaker A and B during production of the gradient. This was avoided by leveling all components of the apparatus and placing beaker B at a slightly higher vertical level than beaker A (easily accomplished with a jackstand).

Calibration of the Gradient

After production of the density gradient, 5 to 10 density standards covering the desired range (1.01 to 1.06 in this work) were added to characterize the gradient. Transfer of a standard to the gradient was facilitated by immersing the bead in a small volume of distilled water. The bristles of a watercolor paintbrush were wetted and the standard was picked up on the tip of the brush. The tip of the brush was dipped in the gradient and the brush gently twisted until the standard fell off and sank. This procedure minimized disturbance of the gradient, prevented small air bubbles from adhering to the outer surface of the standard, and provided a good deal of control in handling and manipulating the beads.

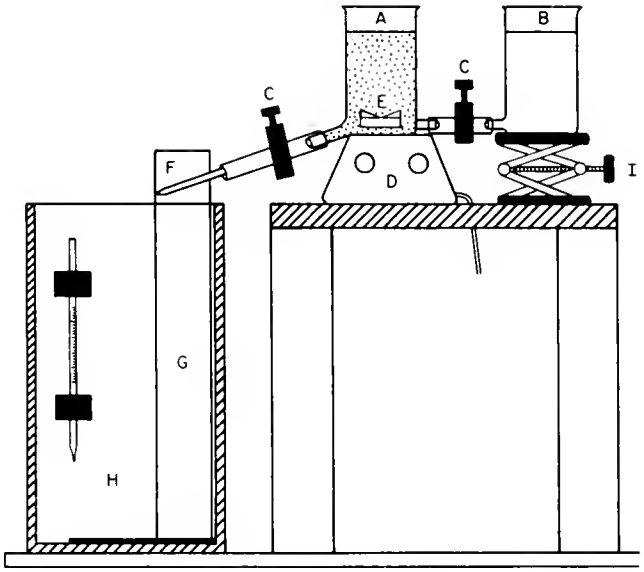


Figure 3. Gradient-making apparatus: (A) beaker containing Na_2SO_4 solution; (B) beaker containing distilled water; (C) pinchcock; (D) magnetic stirrer; (E) stirring disc; (F) Pasteur pipette; (G) gradient cylinder; (H) circulating water bath; and (I) jackstand.

The standards were allowed one-half hour to reach their equilibrium positions. Positions were then measured with a leveled cathetometer to the nearest 0.02 mm. The slope of the gradient (density of the standard versus relative position of the density standards in the gradient) was calculated from this information. The validity of the diver equations is based on a linear gradient (Lovlie and Zeuthen 1962). In particular, the slope of the gradient must be greater than the critical value of 4×10^{-5} mg · μℓ$^{-1}$ · mm^{-1} (Zeuthen and Hamburger 1977). It is recommended that the slope of the gradient be 5 to 10 times this critical value, or somewhere in the range of 2 to 4×10^{-4} mg · μℓ$^{-1}$ · mm^{-1} (Zeuthen and Hamburger 1977), but not less than 0.65×10^{-4} mg · μℓ$^{-1}$ · mm^{-1} (Lovlie and Zeuthen 1962). In the present work, gradient slopes ranged from 2.61 to 2.74×10^{-4} mg · μℓ$^{-1}$ · mm^{-1}. The slope of each gradient was based on a linear regression of density of the standard versus relative position in the gradient of the density standards. In nearly every case, the relationship was virtually

linear (Figure 4). Any gradients that showed too large a deviation from linearity (based on the 99% confidence limits for the line) were discarded. Nonlinearity at the top and bottom of the gradient may be expected due to imperfections in the gradient-making apparatus. It is important, therefore, to confine measurements of diver migration to the middle, linear portion of the gradient, defined by the positions of the lightest and heaviest density standard. It is also important that five or more density standards be used to effectively characterize the gradient (Petersen 1981). It should be noted that once a linear gradient has been produced, any suitable glass sphere may be secondarily calibrated and assigned a density by placing it in the gradient and measuring its equilibrium position (mean of 10 determinations). The density of the sphere may then be estimated on the previously calculated regression equation for the gradient.

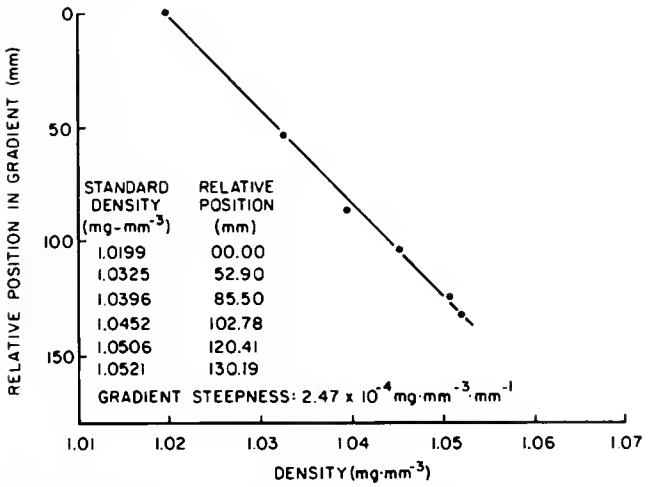


Figure 4. Linear relationship of relative position in the gradient (mm) versus density (mg · $\mu\ell^{-1}$) for six density standards.

Density standards may be reused indefinitely, but must be kept very clean to prevent an increase in weight:volume ratio over time. A dirty standard also tends to retain small bubbles of air on its outside surface when inserted in the gradient. Standards were maintained by rinsing in distilled water immediately after removal from the gradient, then rinsing again with acetone before drying with lint-free tissue paper and storing in dust-free containers. Individual standards were removed from the gradient with a small wire loop described by Moller and Ottolenghi (1964) (see Figure 2G).

Manufacturing and Charging of Divers

The procedures of Nexo et al. (1972) and Zeuthen and Hamburger (1977) were modified to accommodate free-swimming queen conch veligers. Ampulla divers were made from specially ordered precision-bore, thin-walled capillary tubing with an inner:outer diameter ratio of 0.83–0.86. In the present work, tubing with inner diameters of 0.5, 0.9, and 1.3 mm were used to allow for the increasing size of the developing larvae.

The constructing and charging of divers with larvae were combined into one operation. A small length (3 to 4 cm) of capillary tubing of suitable diameter was closed at one end in a microflame and weighed to the nearest 0.1 mg. The tube was then filled with sterilized, filtered (5 μm) and aerated seawater. A single animal was gently pipetted into the tube and allowed to sink to the closed end (for actively swimming animals, gentle persuasion was required). Excess water was withdrawn with the hypodermic needle and the inside of the tube was blotted dry with a small plug of lint-free tissue paper. Enough water was withdrawn to allow free movement of the larva, but minimize diffusion distance within the water compartment of the diver. It was important to dry the inside of the tube as well as possible to provide a clean surface for meniscus movement during diver migration and prevent mixing of the water compartment with the alkali solution in the tail of the diver.

The tail of the diver was then pulled in a microflame (Figure 5). The animal was protected from the heat by a small piece of moist tissue paper. As soon as the capillary heated and began to collapse, it was removed from the flame and quickly drawn out into a long tail by a steady movement of the hands. A little practice at this step resulted in divers that were remarkably similar in size and shape, a necessary condition for the diver equations (Figure 6).

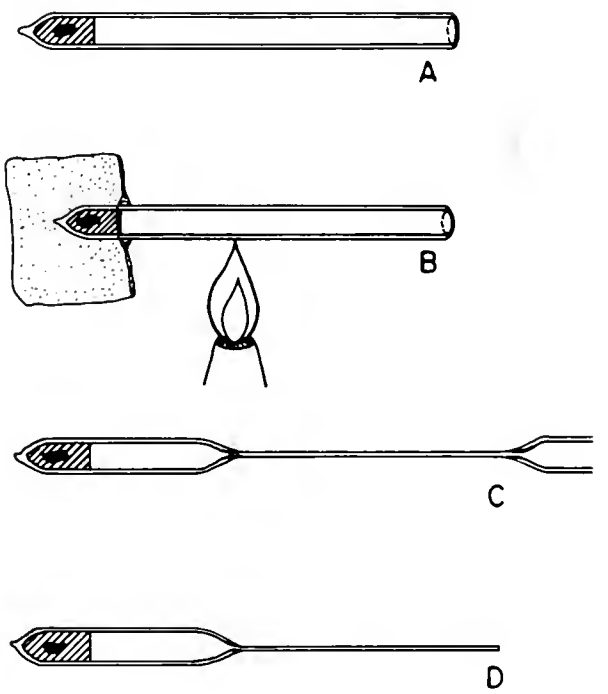


Figure 5. Construction of the ampulla diver: (A) capillary tubing with animal in closed end; (B) heating of the capillary. Animal is protected by a piece of moist tissue paper; (C) drawing out of the tail of the diver; (D) finished diver with tail cut, ready to be charged with NaOH solution (adapted from Petersen [1981], Figure 3).

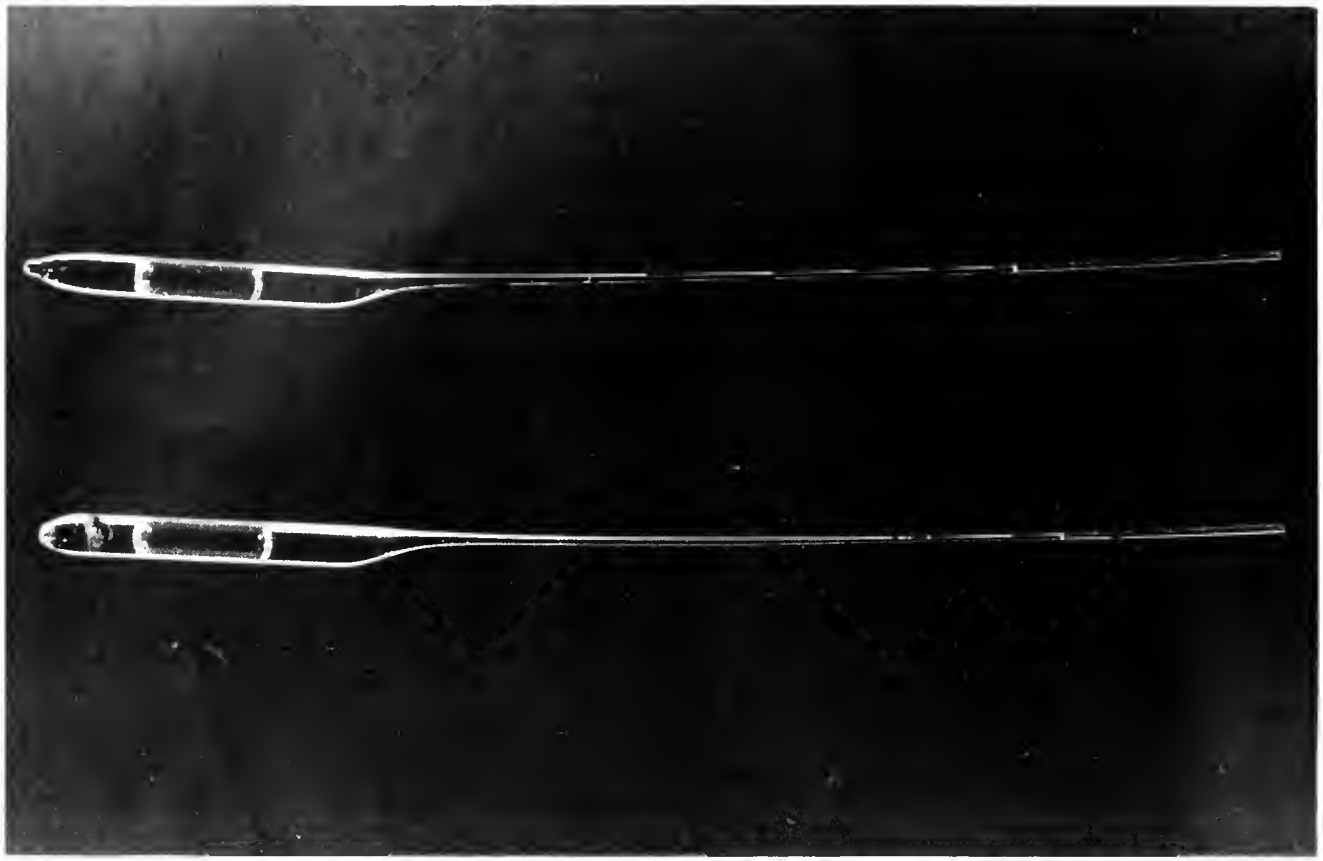


Figure 6. The ampulla diver. The upper diver is the control, the lower diver is the experimental charged with a 20-day-old queen conch larva.

The tail of the diver was cut so that it was 1 to 1.5 times the length of the diver body. The finished diver, regardless of size, should have a tail that is uniform in diameter and cut perpendicular to the long axis of the diver body (Petersen 1981). The excess glass was weighed to the nearest 0.1 mg. When subtracted from the weight of the original piece of capillary tubing, the weight of the diver body (m_{gl}) was determined.

The buoyancy of the divers was adjusted so that their initial positions were in the upper portion of the gradient. This was done while charging the tail of the diver with a weak alkali solution. A diver was transferred to a vacuum tube containing a 0.1-N sodium hydroxide solution that was isotonic with seawater of 32 ppt (Figure 7). The side port of the vacuum tube connected a hand pump via a short length of vacuum tubing. A valve in the hand pump allowed gradual pressure equalization between the gas compartment inside the vacuum tube and the atmopshere. Suction was applied to the gas space in the vacuum tube until air bubbles escaped from the tail of the diver. As suction was slowly released, the escaped air was replaced by sodium hydroxide solution. This procedure was repeated until the desired diver buoyancy was approximated; this point was based on experience and was dependent on the size of the diver and the slope of the gradient.

The diver was then transferred (tail down) to the gradient with a paintbrush. Care was taken to prevent air bubbles from adhering to the outside of the diver. Experimental divers and a suitable control were placed in the gradient (Figure 8). In the present study, nine experimentals and one control were used. The experimenter must be able to uniquely identify all divers. A quick sketch of initial diver placement in the gradient usually sufficed.

Experimental Procedures

Experimental Animals All larvae of *Strombus gigas* were reared from the same egg mass, collected from Biscayne Bay, FL, in August 1983. The egg mass was washed in a 0.5% sodium hypochlorite solution for 45 sec, followed by three 45-sec rinses in fresh seawater. The egg mass was then transferred to a 13-ℓ hatching tank filled with filtered (5μ), aerated seawater treated with 6 mg · ℓ^{-1} chloramphenicol. The hypochlorite wash and chloramphenicol treatment were performed to discourage protozoans and other small organisms collected with the egg mass. Exposure to these conditions does not harm the developing larvae (Siddall 1983). After two days the culture water was exchanged and treated again with chloramphenicol. Incubation temperature for the egg mass was 28°C.

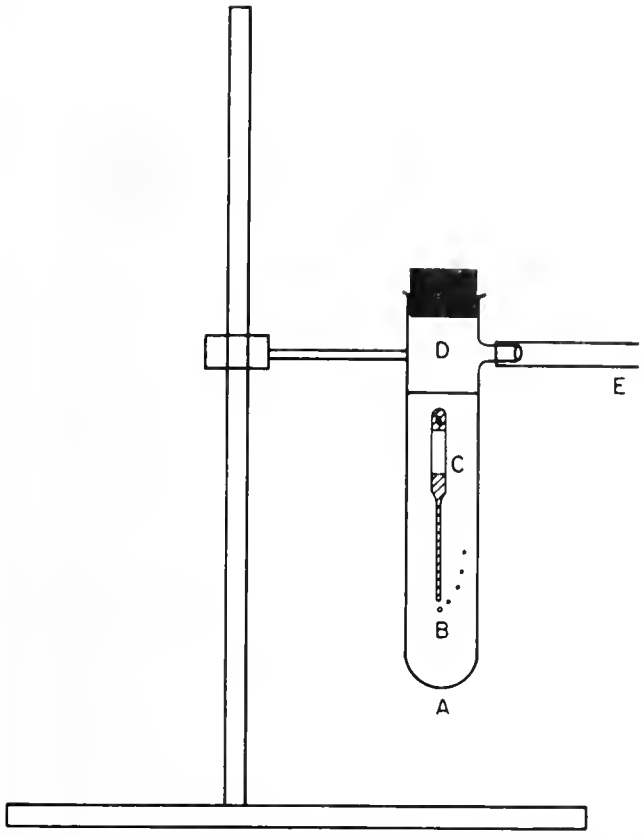


Figure 7. Vacuum tube for charging the tail of a diver with NaOH solution: (A) vacuum tube; (B) 0.1-N NaOH solution; (C) ampulla diver; (D) gas space within the vacuum tube; and (E) vacuum tubing leading to hand pump.

Just prior to hatching (hatch = day 0, about 4 days after collection of the egg mass), the egg mass was transferred to a 370-ℓ culture tank where it hatched. Filtered (5μ), aerated seawater was supplied to the animals on a flowthrough basis for the first three days of planktonic life. On day 3 the first complete water exchange occurred and the animals were fed a mixture of *Isochrysis* aff. *galbana* Parke (Jonc T-Iso), *Dunaliella tertiolecta* Butcher, and *Nannochloris oculata* Droop. Complete water exchanges occurred every other day thereafter. Animals were sampled from this culture on days 4, 7, 10, and 13 of the developmental period.

Sampled animals were allowed to swim in sterilized, filtered, and aerated seawater containing 6 mg · ℓ^{-1} chloramphenicol for 2 to 2.5 hr before the experimental period in an attempt to minimize bacterial respiration, and to provide sufficient time for the larvae to void their gut contents. Each animal was rinsed with sterile seawater immediately prior to enclosure in a diver.

Experimental Measurements Divers were constructed, charged, placed in the gradient, and allowed to equilibrate for 45 min. In this time the divers found their quasi-equilibrium positions and the veligers resumed swimming activity. The relative positions of the gradient surface (H_{surf}), lower air menisci (H_{om}, used in determining V_o), and diver apertures (H_o) were then measured and the barometric pressure recorded. Diver positional changes were measured with a cathetometer every 30 min over a 5-hr (or longer) experimental period. Because relative positional changes were recorded, it was convenient to use the upper tip of the diver as a reference point for measurements. The menisci inside the diver were not used as a reference because their positions may vary during diver migration due to gas-volume changes occurring inside the diver. Upon completion of the experiment, the divers were carefully removed from the gradient by completely enclosing them inside one end of a long, hollow glass tube of sufficient diameter. Once inside, a finger placed over the other end of the tube allowed withdrawal of the diver from the gradient. Density standards were carefully removed with the implement illustrated in Figure 2G.

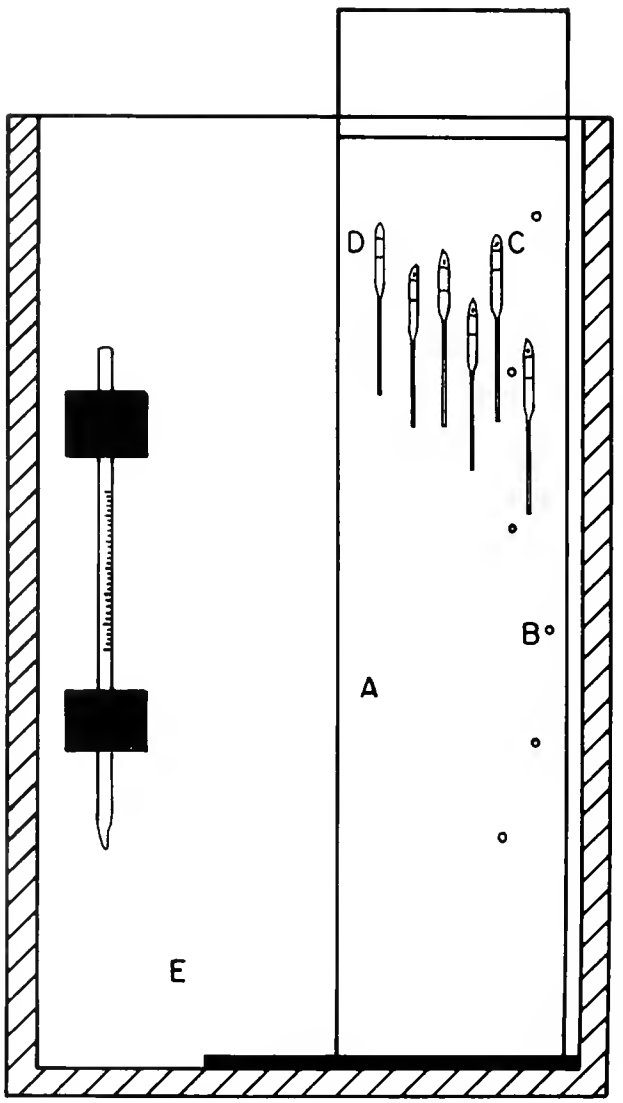


Figure 8. Open gradient-diver assembly: (A) gradient cylinder containing density gradient; (B) density standard; (C) experimental diver; (D) control diver; and (E) circulating water bath.

At this point, the internal volume of each diver was determined. This was accomplished by gently boiling each diver at low pressure in distilled water. When the diver was filled with water, it was weighed to the nearest 0.1 mg (m_f). The internal volume of the diver was determined via Eq. 4.

Each animal was carefully removed from its ampulla and frozen immediately. To prepare the larval tissue for weighing, the shell was removed by decalcification in an equal volume-water dilution of a standard decalcifying reagent (RDO, Dupage Kinetic Laboratories, Inc., Plainfield, IL). The tissue was subsequently rinsed with distilled water, dried over anhydrous calcium sulfate at 60°C for 48 hr, and stored individually over dessicant in small vials. All animals were weighed on a quartz fiber balance to the nearest 0.01 μg (Lowry and Passonneau 1972).

RESULTS

Table 1 presents the oxygen uptake rates in $\mu\ell\ O_2 \cdot hr^{-1} \cdot 10^{-3}$ for all larvae sampled, arranged by age class. Each value represents the mean oxygen uptake rate for an individual over a 5-hr experimental period, recorded every 30 min. During this time, nearly all individuals were observed to swim actively. For the purposes of this paper, only actively swimming animals were considered. Corresponding larval weight (μg) and weight-specific respiration rate ($\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g$ dry tissue) for each animal are presented in Table 2.

TABLE 1.

Oxygen uptake rates ($\mu\ell\ O_2 \cdot hr^{-1} \cdot 10^{-3}$) per larva, arranged by age class.

Age (Days)	4	7	10	13
n	9	9	9	9
Oxygen Uptake	6.659	13.209	20.307	29.537
	4.502	9.838	14.105	31.397
	5.788	9.369	13.514	32.775
	5.639	12.220	18.161	43.021
	5.533	9.869	19.401	31.292
	6.638	12.440	16.715	32.682
	5.473	9.769	27.011	27.091
	5.638	11.120	22.001	27.698
	5.823	8.424	20.421	27.630
$\bar{x}$	5.744*	10.695*	19.082*	31.458*
SD	0.645	1.623	4.139	4.854

*Student-Newman-Keuls multiple range test: $\alpha = 0.05$

Summary of statistical tests:

One-way ANOVA:

Calculated $F = 104.114$

$F_{0.05(1),3,32} = 2.90$

Reject H_0: $\mu_4 = \mu_7 = \mu_{10} = \mu_{13}$ $P < 0.005$

Variabilities around the mean oxygen-uptake rates for each age group were subjected to a one-way analysis of variance (ANOVA). At $\alpha = 0.05$, the null hypothesis of equal mean oxygen-uptake rates for all age groups was rejected. A Student-Newman-Keuls multiple range test (SNK test) was then performed to determine among which age groups differences existed. The mean oxygen-uptake rates for 4-, 7-, 10-, and 13-day-old animals were all found to be significantly different at the $\alpha = 0.05$ level; these rates were 5.744, 10.695, 19.082, and 31.458 $\mu\ell\ O_2 \cdot hr^{-1} \cdot 10^{-3}$, respectively. A summary of these statistical tests may be found in Table 1.

Similar tests were applied to the weight-specific respiration data of Table 2. Again, at $\alpha = 0.05$, the null hypothesis of equal mean-weight-specific respiration rates for all age groups was rejected. The SNK test, however, discerned a significant difference in mean weight-specific respiration rates only between 13- and 10-day-old animals. In all other pairings the null hypothesis of equal mean-weight-specific respiration rates could not be rejected. A summary of these statistical tests is presented in Table 2.

Calculations were performed to determine the change in ambient oxygen levels between the beginning and end of each experimental period. In these calculations, the smallest volumes (both gas space and biological medium) and the largest respiration rates observed for each day were used. Although this combination did not actually occur in any given diver, it resulted in a "worst case" estimate of declining ambient pO_2 available to the experimental animals. At no time did the ambient pO_2 level fall below 80% of its initial value.

DISCUSSION

Gradient-diver respirometry offers a number of advantages when determining respiration rates of small aquatic organisms. In particular, it has the flexibility to allow measurements on a relatively wide range of animal sizes while retaining sufficient sensitivity to work with individual organisms. The ability to measure individual respiration rates is important because it allows individual variability in the rates to be assessed. Adjusting the diver size to fit the organism is a relatively simple matter, although techniques for constructing and charging the divers depend somewhat on the size and type of organism under study. Petersen (1981) discussed gradient-diver respirometry modified for terrestrial microarthropods and Nexo et al. (1972) described alternate techniques of charging divers with large and small aquatic organisms. The charging technique described in the **MATERIALS AND METHODS** section of this paper worked extremely well for single eggs of *Strombus gigas* as well as metamorphosing veliger larvae.

The sensitivity of gradient-diver respirometry has been adequately demonstrated by other workers (Zeuthen and Hamburger 1977, Hamburger 1981, Petersen 1981) and has been shown to be inversely proportional to diver size (Nexo et al. 1972). In the present study, a respiration rate of $4.502 \times 10^{-3} \mu\ell\ O_2 \cdot hr^{-1}$ was detected for a 4-day-old veliger larva of 1.04 μg dry-tissue weight. This corresponds to a weight-specific respiration rate of $4.33 \times 10^{-3} \mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$.

TABLE 2.

Larval dry-tissue weight (μg) and weight-specific respiration rate ($\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g\ dry\ tissue^{-1}$) for each larva, arranged by age class.

Age (Days)	4		7		10		13	
n	9		9		9		9	
	Weight μg	Respiration $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$	Weight μg	Respiration $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$	Weight μg	Respiration $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$	Weight μg	Respiration $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$
	0.94	7.08×10^{-3}	2.21	5.98×10^{-3}	2.47	8.22×10^{-3}	5.73	5.15×10^{-3}
	1.04	4.33×10^{-3}	1.92	5.12×10^{-3}	2.66	5.30×10^{-3}	7.21	4.35×10^{-3}
	1.03	5.62×10^{-3}	1.51	6.20×10^{-3}	2.21	6.11×10^{-3}	5.26	6.23×10^{-3}
	1.02	5.53×10^{-3}	2.16	5.66×10^{-3}	2.79	6.51×10^{-3}	9.84	4.37×10^{-3}
	1.01	5.48×10^{-3}	1.92	5.14×10^{-3}	2.36	8.26×10^{-3}	6.19	5.05×10^{-3}
	1.03	6.44×10^{-3}	1.56	7.97×10^{-3}	2.48	6.74×10^{-3}	5.07	6.45×10^{-3}
	0.83	6.59×10^{-3}	1.96	4.98×10^{-3}	3.83	7.05×10^{-3}	5.84	4.64×10^{-3}
	1.02	5.53×10^{-3}	1.60	6.95×10^{-3}	3.09	7.12×10^{-3}	6.59	4.20×10^{-3}
	0.94	6.19×10^{-3}	1.48	5.69×10^{-3}	3.49	5.85×10^{-3}	5.65	4.89×10^{-3}
$\bar{x}$	0.98	5.86×10^{-3}	1.81	5.96×10^{-3}	2.82	6.79×10^{-3}	6.37	5.04×10^{-3}
SD	0.06	0.80	0.28	0.97	0.55	1.00	1.46	0.81

Student-Newman-Keuls multiple range test: $\alpha = 0.05$

Age (Day)	13	4	7	10
$\bar{x}$ ($\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1} \cdot 10^{-3}$)	5.04	5.86	5.96	6.79

Summary of statistical tests:

One-way ANOVA:

Calculated $F = 5.75$

$F_{0.05(1),3,32} = 2.90$

Reject H_0: $\mu_4 = \mu_7 = \mu_{10} = \mu_{13}$ $\quad 0.0025 < P < 0.005$

Smaller divers may be constructed. I have measured a respiration rate of 1.19×10^{-3} $\mu\ell\ O_2 \cdot hr^{-1}$ ($V_O = 1.23$ $\mu\ell$) in a single 2-day-old egg of *S. gigas*. Lovlie (1968) used very small divers ($V_O = 0.03$ $\mu\ell$) to study photosynthesis in single cells of *Ulva mutabilis* Föyn. At the other extreme, divers with $V_O = 10$ to 15 $\mu\ell$ were used for respiration studies of single eggs of *Drosophila melanogaster* (Meigen) (Lints et al. 1967) and Hamburger and Zeuthen (1974) used divers with $V_O = 50$ $\mu\ell$ to study mitotic cycles in single cleaving frog eggs.

Gradient-diver respirometry, in general, is also quite precise, although overall precision may be hindered by difficulty in controlling activity patterns in the organisms under study. This is particularly true with free-swimming organisms such as molluscan larvae. The technique outlined in this paper enabled me to distinguish, on the basis of mean-oxygen-uptake rates, that queen conch veligers differed by as little as three days in age. Variability in the respiration rates given in Tables 1 and 2 was probably caused by differences in swimming activity of each animal during the experimental period and most likely resulted in the difference in weight-specific respiration rates between 13- and 10-day-old veligers. Although the data presented are for "actively swimming" animals, this activity was assessed only at each 30-min observation and no attempt was made to discriminate faster from more slowly moving animals. A dramatic difference, however, is seen in the cumulative oxygen uptake of actively swimming animals compared to animals with velar lobes only partially extended (Figure 9).

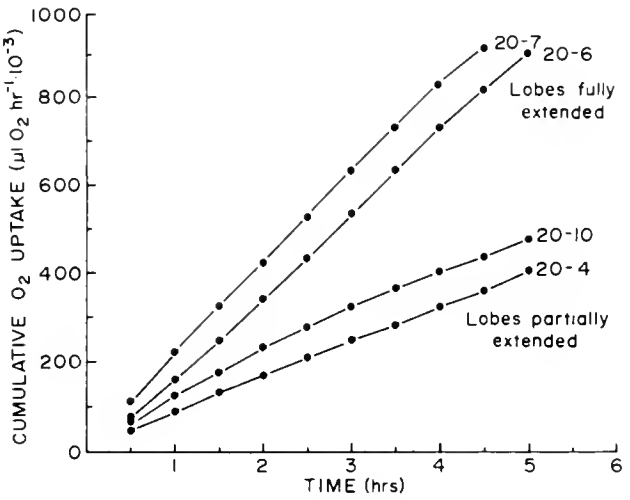


Figure 9. Cumulative oxygen uptake ($\mu\ell\ O_2 \cdot hr^{-1} \cdot 10^{-3}$) versus time in 20-day-old veligers of *Strombus gigas* with velar lobes fully and partially extended.

Differences in activity patterns become especially problematical when the sampled population is small or very

fine discrimination in respiration rates is required. Increasing the sample size for any given experiment will tend to offset these problems. It is possible to operate two or more gradients in tandem. Any number of divers may be placed in one gradient, although experience has shown that 9 to 10 experimentals and at least one control diver are optimal.

The respiration rates obtained for veligers of *Strombus gigas* are comparable to published values for molluscan larvae using other microrespirometric techniques. Pechenik (1980), using an all-glass differential microrespirometer (Grunbaum et al. 1955), observed a respiration rate of 4.67×10^{-3} $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$ for larvae of *Ilyanassa obsoleta* (Say) of 1.04 μg dry-tissue weight at 20°C. His value was obtained from respiration and weight measurements based on grouped individuals, although the exact number of animals was not indicated. No mention was made of activity levels within the microrespirometer; presumably, interaction of individuals occurred. Vernberg (1972) and Vernberg and Vernberg (1975), using Cartesian-diver microrespirometry on 1-day-old larvae of *I. obsoleta*, reported a respiration rate of about 2 to 2.5 $\mu\ell\ O_2 \cdot mg^{-1}$ total dry weight $\cdot hr^{-1}$ at 25°C, based on 6 to 12 replicates with one veliger per diver. Activity levels of the veligers were not observed. Assuming shell weight is approximately 80% of total dry weight in gastropods, those 1-day-old larvae of *I. obsoleta* had a dry-tissue weight of about 0.5 μg and a weight-specific respiration rate of 5×10^{-3} $\mu\ell\ O_2 \cdot hr^{-1} \cdot \mu g^{-1}$. Both the value given by Pechenik (1980) and the estimated value from Vernberg and Vernberg (1975) agree well with the mean weight-specific respiration rate of 5.86×10^{-3} $\mu\ell O_2 \cdot hr^{-1} \cdot \mu g$ for 4-day-old conch veligers (mean weight, 0.98 μg).

Many respirometric techniques, especially those associated with polarographic oxygen electrodes, require stirring of the biological medium during measurements. Organisms that cannot tolerate this agitation due to physical damage or whose normal respiratory activity is interrupted during measurements by withdrawal into a shell, for example, are impossible to work with using these methods. At worst, the animals do not survive the experimental treatment and, at best, the results are difficult to interpret due to the influence of stirring on the respiration rate itself. Davenport (1976) described a technique for measurement of oxygen consumption in small aquatic organisms using a Clarke-type oxygen electrode that relied on animal movements to mix the biological medium. Although the technique seemed to work well when enough animals were present to stir the biological medium, it was not clear whether respiration rates in individual small gastropod or bivalve larvae could be detected.

The influence of experimental manipulations and procedures on respiration rates are, of course, common to all respirometric techniques. In most cases, they are difficult if not impossible to sort out. They can, however, be minimized to a great extent. In nearly all cases, the animals in this study appeared to suffer no adverse effects from experimental manipulations. Active swimming was generally resumed shortly after placement of the diver in the gradient. Free-swimming molluscan larvae are particularly suited to gradient-diver respirometry. Without the effects of stirring, the animals are able to swim inside the diver without interruption of normal respiratory activity. At the same time, movement of the animal inside the diver facilitates diffusion of gases into the gas space from the water compartment.

The technique also lends itself well to automatic recording as described by Lovlie and Zeuthen (1962) and Zeuthen and Hamburger (1977). After preparing the gradient and divers, a camera may be placed in such a way to take sequential photographs of diver migration. The experimenter may then leave the apparatus during the experimental period. Automatic recording, however, reduces the sensitivity of the technique because the resolution of diver migration rates with a camera is not as fine as can be obtained with a cathetometer.

There are disadvantages to the gradient-diver technique. Although constant attention (as in the Cartesian-diver system) is not required, it remains a time-intensive technique. In the present study, approximately 4 to 5 hr were required for pre- and postexperimental preparation. This included 2 to 2.5 hr to mix the gradient, 30 to 60 min to make and charge the divers, 60 min to obtain mf for all divers, and 60 min for system maintenance (cleaning density standards, gradient tube, etc.) and other small operations. The time required is not necessarily additive. The gradient may be mixed while other operations are initiated, for example. In fact, the gradient may even be mixed the day before since it has been shown to be very stable over time (Lovlie and Zeuthen 1962). The length of the experimental period is variable, depending on objectives.

Finally, some skill and experience are required to successfully manufacture and charge ampulla divers. A reasonable amount of practice overcomes this difficulty.

These disadvantages aside, the gradient-diver respirometer allows measurement of individual respiration rates in very small aquatic and terrestrial organisms which may not be successfully obtained with other microrespirometric techniques. The technique is particularly suitable for ecological applications where an assessment of variability in individual respiration rates is desired. Compared to other microrespirometric techniques, the gradient-diver respirometer is relatively inexpensive; most components may be made from ordinary laboratory equipment and glassware.

ACKNOWLEDGMENTS

I am indepted to Drs. Peter Lutz and Scott Siddall for their encouragement of and comments on this manuscript. I also thank Dr. Dalton Dietrich, Department of Neurology,

University of Miami Medical School, for the use of his quartz fiber balance.

Finally, I express my appreciation to the Jessie Smith Noyes Foundation, New York, NY, for support in the form of a fellowship, without which this study would not have been possible.

REFERENCES CITED

Boell, E. J. & S. C. Shen. 1950. Development of cholinesterase in the central nervous system of *Amblystoma punctatum*. *J. Exp. Zool.* 113:583–599.

Davenport, J. 1976. A technique for the measurement of oxygen consumption in small aquatic organisms. *Lab. Pract.* 25:693–695.

Grunbaum, B. W., B. V. Siegel, A. R. Schulz & P. L. Kirk. 1955. Determination of oxygen uptake by tissue growth in an all-glass microrespirometer. *Mikrochim. Acta* 6:1069–1075.

Hamburger, K. 1981. A gradient diver for measurement of respiration in individual organisms from the micro- and meiofauna. *Mar. Biol. (Berl.)* 61:179–183.

_____ , B. Kramhoft, S. B. Nissen & E. Zeuthen. 1977. Linear increase in glycolytic activity through the cell cycle of *Schizosaccharomyces pombe*. *J. Cell. Sci.* 24:69–79.

Hamburger, K. & E. Zeuthen. 1974. Recording mitotic cycles in single cleaving frog eggs. Gasometric studies with the Gradient Diver. *C. R. Trav. Lab. Carlsberg* 39:415–432.

Holter, H. 1943. Technique of the Cartesian Diver. *C. R. Trav. Lab. Carlsberg Ser. Chim.* 24:399–478.

_____ . 1961. The Cartesian Diver. Danielli, J. F., ed. *General Cytochemical Methods*. New York, NY:Academic Press. 93–129.

_____ & E. Zeuthen. 1966. Manometric techniques for single cells. Oster, G. and Pollister, A. W., eds. *Physical Techniques in Biological Research*. New York, NY: Academic Press. Vol. III: 251–317.

Linderstrom-Lang, K. 1937. Principle of the Cartesian Diver applied to gasometric technique. *Nature* 140:108.

_____ . 1943. On the theory of the Cartesian Diver microrespirometer. *C. R. Trav. Lab. Carlsberg Ser. Chim.* 24:333–398.

Lints, C. V., F. A. Lints & E. Zeuthen. 1967. Respiration in *Drosophila*. I. Oxygen consumption during development of the egg in genotypes of *Drosophila melanogaster* with contribution to the Gradient Diver Technique. *C. R. Trav. Lab. Carlsberg* 36:35–66.

Lovlie, A. 1968. Genetic control of division rate and morphogenesis in *Ulva mutabilis* Föyn. *C. R. Trav. Lab. Carlsberg* 34:77–168.

_____ & E. Zeuthen. 1962. The Gradient Diver – a recording instrument for gasometric micro-analysis. *C. R. Trav. Lab. Carlsberg* 32:513–534.

Lowry, O. H. &. J. V. Passonneau. 1972. The quartz fiber fishpole balance. *A Flexible System of Enzyme Analysis*. New York, NY: Academic Press. 237–249.

Luxton, M. 1975. Studies on the oribatid mites of a Danish beech wood soil. II. Biomass, calorimetry, and respirometry. *Pedobiologia* 15:161–200.

Moller, K. M. & P. Ottolenghi. 1964. The manufacture of small glass floats for calibrating density gradients. *C. R. Trav. Lab. Carlsberg* 34:169–185.

Nexo, B. A., K. Hamburger & E. Zeuthen. 1972. Simplified microgasometry with Gradient Divers. *C. R. Trav. Lab. Carlsberg* 39:33–63.

Pechenik, J. A. 1980. Growth and energy balance during the larval lives of three prosobranch gastropods. *J. Exp. Mar. Biol. Ecol.* 44:1–28.

Petersen, H. 1981. Open gradient diver respirometry modified for terrestrial microarthropods. *Oikos* 37:265–272.

Siddall, S. 1983. Biological and economic outlook for hatchery production of juvenile queen conch. *Proc. Gulf Caribb. Fish. Inst.* 35:46–52.

Steigen, A. L. & R. Z. Klekowski. 1977. Oxygen consumption in Collembola from two forest biotypes. *Ekol. Pol.* 25:447–454.

Vernberg, W. B. 1972. Metabolic-environment interaction in marine plankton. Battaglia, G., ed. *Fifth European Marine Biological Symposium*. Piccin Editore, Padua, Italy. 189–196.

_____ & F. J. Vernberg. 1975. The physiological ecology of larval *Nassarius obsoletus* (Say). Barnes, H., ed. *Ninth European Marine Biological Symposium*. Aberdeen, U.K.: University Press. 179–190.

Webb, N. R. 1969. The respiratory metabolism of *Nothrus sylvestris* Nicolet. *Oikos* 20:294–299.

Zajicek, J. & E. Zeuthen. 1961. Quantitative determination by a special "ampulla diver" of cholinesterase activity in individual cells, with notes on other uses of the method. Danielli, J. F., ed. *General Cytochemical Methods*. New York, NY:Academic Press. 131–152.

Zeuthen, E. 1947. Body size and metabolic rate in the animal kingdom with special regard to the marine micro-fauna. *C. R. Trav. Lab. Carlsberg Ser. Chim.* 26:17–161.

_____ . 1949. Oxygen consumption during mitosis; experiments on fertilized eggs of marine animals. *Am. Nat.* 83:303–318.

_____ . 1953. Growth as related to the cell cycle in single-cell cultures of *Tetrahymena piriformis*. *J. Embryol. Exp. Morphol.* 1:239–249.

_____ & K. Hamburger. 1972. Mitotic cycles in oxygen uptake and carbon dioxide output in the cleaving frog egg. *Biol. Bull. (Woods Hole)* 143:699–706.

_____ . 1977. Microgasometry with single cells using ampulla divers operated in density gradients. Glick, D. and Rosenbaum, R. R., eds. *Techniques of Biochemical and Biophysical Morphology*. New York, NY: John Wiley and Sons, Inc. 58–79.

Journal of Shellfish Research, Vol. 4, No. 1, 17–21, 1984.

BREEDING BEHAVIOR OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ HELD IN A NATURAL ENCLOSED HABITAT

MEGAN DAVIS, BRENT A. MITCHELL AND
JESSICA L. BROWN
Foundation for PRIDE
7600 SW 87th Ave.
Miami, Florida 33173

ABSTRACT An enclosed, natural breeding habitat for the queen conch *Strombus gigas* Linné was established and monitored during the 1981 and 1982 breeding seasons in the Turks and Caicos Islands. Breeding behavior of conchs was studied at a site from which egg masses were collected for mariculture research. The egg-laying season extended from late March to early September, with a distinct seasonal variation in the number of egg masses produced. The mean numbers of egg masses produced per female per month for 1981 and 1982 were 1.2 and 1.7, respectively.

KEY WORDS: Queen conch, *Strombus gigas*, reproduction, mariculture

INTRODUCTION

The breeding behavior of the queen conch *Strombus gigas* Linné has been examined by several researchers (Robertson 1959, Randall 1964, D'Asaro 1965, Fredrick 1975, Berg 1976, Hesse 1976, Brownell 1977). Sexual maturity occurs at 3 to 3.5 years, after the flared aperture lip of the conch is fully formed. The average life span is 6 years (Berg 1976); therefore, the average reproductive span is about 2.5 to 3 years. The queen conch is diecious with internal fertilization (Robertson 1959). Copulation, which occurs several weeks before spawning, was observed by D'Asaro (1965) who demonstrated that sperm is viable in the seminal receptacle for several weeks. Copulation and spawning can also occur at the same time (Randall 1964, Hesse 1976, Brownell 1977). *Strombus gigas* can lay several egg masses after a single copulation (D'Asaro 1965, Ernesto Weil M., Fundacion Cientifica Los Roques, Caracas, Venezula; pers. comm. 1982). Females usually deposit the egg mass on clean coral sand with a low-organic content (D'Asaro 1965). The number of eggs per mass ranges from 313,000 to 485,000 (Robertson 1959, Randall 1964). Robertson (1959) described the typical egg mass and capsules of *S. gigas*.

The timing and duration of the breeding period for *S. gigas* vary according to location and season. In the Turks and Caicos Islands, breeding begins in March and lasts through September (Hesse 1976). As far as we could determine, no data have been collected on fecundity of individual conchs throughout a breeding season either in the wild or in an enclosure.

The purpose of this study was to enclose a breeding population of *Strombus gigas* in a natural habitat to: (1) obtain data on reproductive behavior and fecundity, and (2) provide a reliable source of egg masses for a hatchery.

MATERIALS AND METHODS

An underwater, enclosed breeding arena for queen conchs was constructed in a conch-breeding habitat within the Pine Cay barrier reef, 2.5 km northwest of the island (Figure 1). Mature individuals of both sexes were transferred to the site in 1981 and again in 1982, and were monitored from mid-June to September in 1981 and from late March to early September in 1982.

The 1,600-m^2 enclosure was located in 6 m of water on sand and coral rubble that was covered with algae and 75% enclosed by a natural coral reef (Figure 2, Table 1). Two natural openings through the reef were sealed with 1- × 25-m nets with lead weights attached at the bottom and floats at the top. After experimentation in 1981 with monofilament and nylon net material, orange polypropylene was chosen in 1982. The strength and color of the polypropylene helped to minimize damage caused by marine animals that might become entangled in the net.

The selected site contained a natural breeding population until it was fished out in 1980. In 1981 and 1982, with the cooperation of the Turks and Caicos government, this site was designated as a protected breeding ground. In June 1981, the breeding site was sealed and stocked with fifty, 4- to 6-year-old, mature conchs (1 per 32 m^2). In March 1982, the site was reconstructed and restocked with 100 to 120 mature conchs (1 per 16 m^2 to 1 per 13.3 m^2, respectively). The density of a natural, undisturbed population of juvenile and adult conchs near Six Hills Cay, Turks and Caicos Islands, is 1 conch per 10.7 m^2 (Hesse 1976); our stocking density was within this range. The sex ratio in the enclosure during both years was approximately 1:1. This reflected the natural 1:1 sex ratio of adult conchs in the wild (Randall 1964, Fredrick 1975, Berg 1976, Brownell 1977).

Sexually mature individuals with a fully developed lip and a sufficient spire (to permit tagging) were collected by free diving around patch reefs and large limestone boulders which were devoid of coral life. The collection site had a substrate of coarse sand and macroalgal flora dominated by

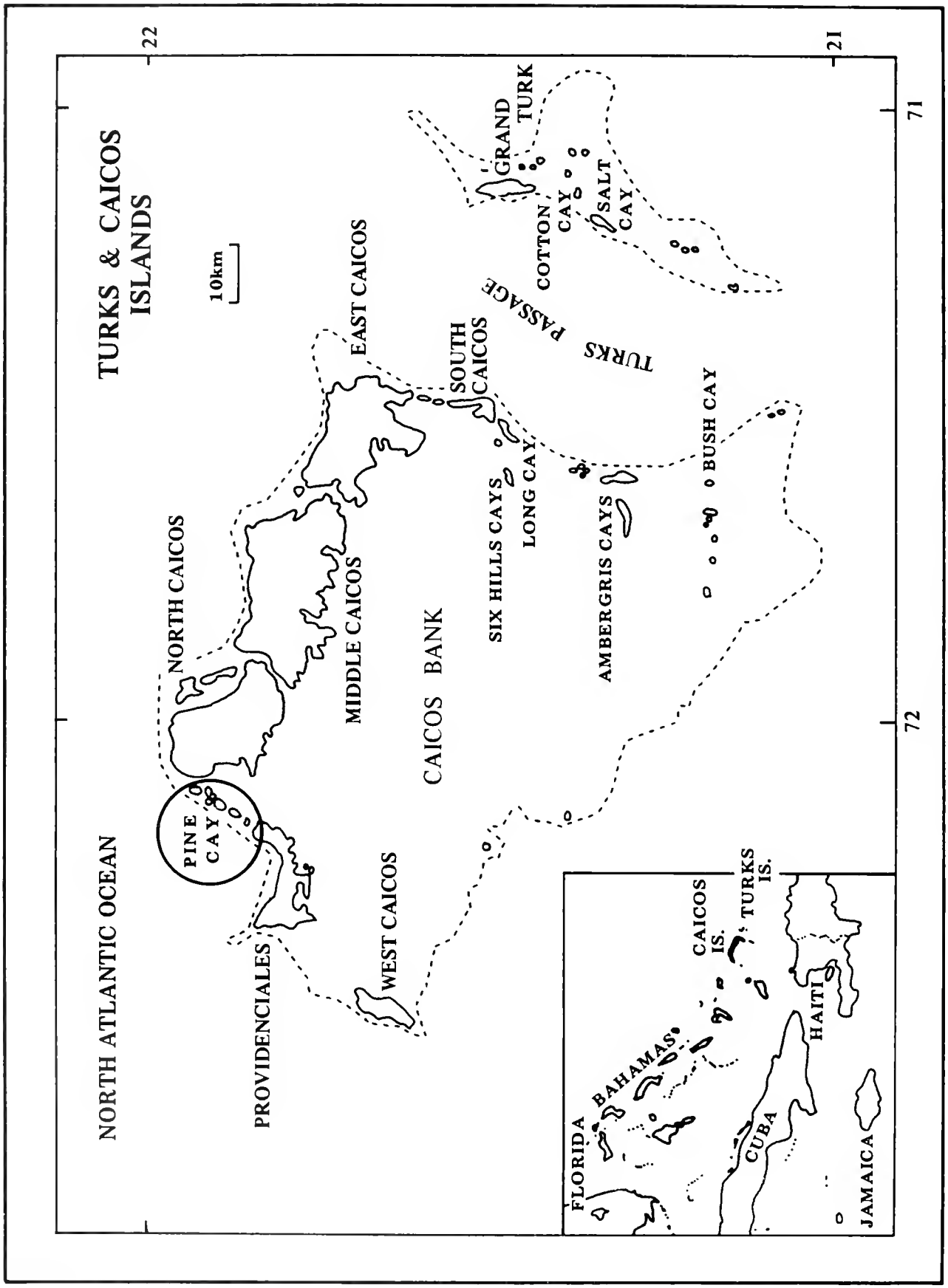


Figure 1. Turks and Caicos Islands (Davis and Hesse 1982).

Laurencia poitei (Lamouroux). Each conch was tagged with a 12- × 6-cm yellow, numbered, plastic tag that was attached to the spire with a plastic pull tie. Tagged conchs, which were exposed to the air for less than 2 hours, showed no sign of stress after transfer to the enclosed site. In March 1982, two days after transfer, these conchs were observed copulating with conchs from different collection areas and laying egg masses.

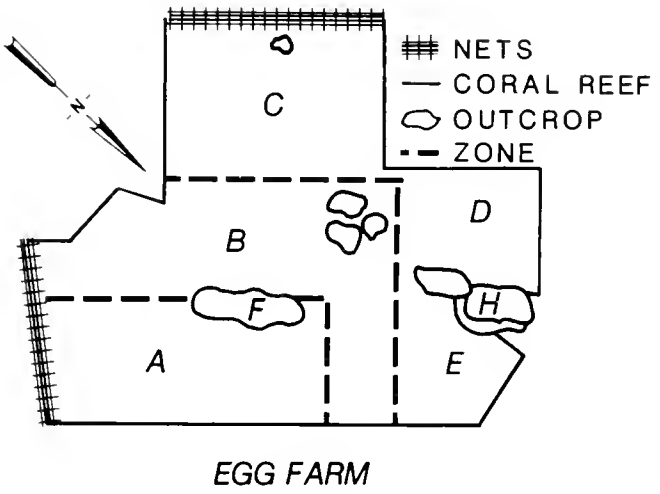


Figure 2. PRIDE Egg Farm located in Pine Cay barrier reef (Davis and Hesse 1982).

In 1981, sex was determined by placing a tagged conch on its side and noting gender when the animal came out of the shell to right itself. In 1982, sex was simply determined by observing and recording breeding behavior, i.e., pairing, copulating, and egg laying, for each tagged animal.

Two or three times a week, SCUBA-equipped researchers systematically surveyed the enclosure for tagged conchs, recorded their presence, noted pairing and copulating, and inspected the area under the anterior aperture lip for egg masses. Temperature, water conditions, and wind direction were recorded. Underwater observations were made for 62 hours in 1981 and for 92 hours in 1982.

Intervals between visits to the breeding site were based on the observation that females take from 24 to 36 hours to lay an egg mass (Randall 1964, D'Asaro 1965) and that eggs hatch after 3 to 5 days (Robertson 1959, Randall 1964, D'Asaro 1965, Hesse 1976, Brownell 1977, Davis 1982). Observations of all egg-laying activity were made at a minimum of 3- to 4-day intervals. Females laying egg masses and completed egg masses no longer under the females were recorded and marked with colored weights to ensure that the egg masses were not recounted. Firm, freshly laid egg masses were collected for the hatchery-rearing efforts.

TABLE 1.

Egg farm substrates and macroalgae.

Zone	Substrate	Macroalgae	
		Dominant	Other
A	Large rocks, fragments of dead staghorn coral and conch shells, coral rubble, sand patches, silt covering	*Microdictyon* sp. *Digenia simplex* (Wulfen) *Cladophoropsis membranacea* (C. Agardh)	*Sargassum* sp. *Halimeda* sp. *Rhipocephalus phoenix* (Solander) *Acicularia schenskii* (Möbius) *Acetabularia* sp.
B	Small rocks, fragments of coral and conch shells, small sand patches, silt covering	*Microdictyon* sp. *Acetabularia* sp. *Acicularia schenskii* (Mobius) *Cladophoropsis membranacea* *Digenia simplex*	*Sargassum* sp. *Halimeda* sp. *Padina haitiensis* (Thiuy)
C	Majority sand, scattered coral rubble, small rocks, and fragments of conch shells	*Acetabularia* sp. *Acicularia schenskii* *Batophora oerstedi* J. Agardh *Digenia simplex* *Cladophoropsis membranacea*	*Sargassum* sp. *Anadyomene stellata* (Wulfen)
D	Coral rubble, rocks, knocked conch shells, silt covering	*Microdictyon* sp. *Cladophoropsis membranacea*	*Halimeda* sp. *Dictyota* sp. *Sargassum* sp. *Padina haitiensis*
E	Large rocks, coral rubble, few sand patches, hard surface, silt covering	*Microdictyon* sp. *Digenia simplex* *Cladophoropsis membranacea*	*Sargassum* sp. *Dictyota* sp.
F & G	Rocks, coral reef	*Sargassum* sp. *Microdictyon* sp. *Cladophoropsis membranacea*	
H	Rocks, coral reef, coral rubble	*Microdictyon* sp. *Halimeda* sp. *Digenia simplex* *Cladophoropsis membranacea*	*Sargassum* sp. *Turbinaria turbinata* (Linnaeus)

RESULTS AND DISCUSSION

Egg-mass productivity of the conchs showed seasonal variations, with a midseason peak in the number of egg

masses produced. Temperature and weather conditions were correlated with egg-laying activity. In 1982, water temperature was recorded below a thermocline, 1 to 2 m from the bottom. Water temperature averaged 27°C from March to June and 29°C from July to September with peaks at 30.5°C. Figure 3A presents data from the seond half of the 1981 breeding season, while Figure 3B presents data from the complete 1982 breeding season with a visual-fit line representing average water temperature. The graphs illustrate seasonal variation in egg-mass production and the number of egg masses per female per observation day. The low data points circled on Figure 3B occurred on stormy days when the storm surges may have decreased egg-laying activity. During the summer months southeastern trade winds predominate. When winds shift to the north they are accompanied by storms and/or increased wave action, which frequently cause the sand substrate to shift. At those times, many conchs in the breeding arena were observed to be partially buried in the sand. A few individuals were found completely buried for up to 2 weeks after a storm has passed. The majority of egg masses were found in Zones B and C (Figure 2), where sand and coral rubble substrates predominated. Females were frequently noted laying their egg masses against small inclines in those substrates. Hesse (1976) observed this behavior at Six Hills Cay, Turks and Caicos Islands. As the female deposited the egg mass she covered the strands with sand and small rubble particles. Other observations (Davis et al., unpublished data) in the Turks and Caicos Islands have shown that substrate type is a very important factor for egg laying.

In July 1984, 100 mature conchs were held for 30 days in a different enclosure in shallow, 1-m-deep water, with a substrate bottom of sandy mounds, fine sand particles, and calcareous algae. Mature conchs had been noted in that area, however, they were not laying egg masses. During that 30-day period none of the conchs in the new enclosure copulated or laid eggs; however, once the conchs were transferred to a site similar to the 1981 and 1982 breeding site that contained large, coarse sand particles, coral rubble and low amounts of organics, they began laying egg masses within 2 days.

The first egg mass of the 1982 season was observed on March 22, the last on September 8, after which breeding activity ceased. Robertson (1959), Randall (1964), D'Asaro (1965), and Hesse (1976) attributed the onset and cessation of conch reproduction to changes in temperature and/or weather. A combination of weather and temperature probably determined the reproductive period at the breeding site during this study.

Occasionally, individuals were observed laying egg masses while copulating. Certain males and females were observed to have a higher frequency of copulation and pairing than other conchs in the enclosure (Davis 1982). Periodic visits to the site were not adequate to make a direct correlation between specific instances of breeding activity and egg-mass production, i.e., because copulation occurs as much as several weeks before egg laying (D'Asaro 1965, Hesse 1976) and because females may lay more than one egg mass per copulation (D'Asaro 1965, Ernesto Weil M., Fund. Cient. Los Roques, Caracas, Venezuela; pers. comm. 1982). However, reproduction data acquired at the breeding site do indicate that copulatory activity increased during the middle of the 1982 season.

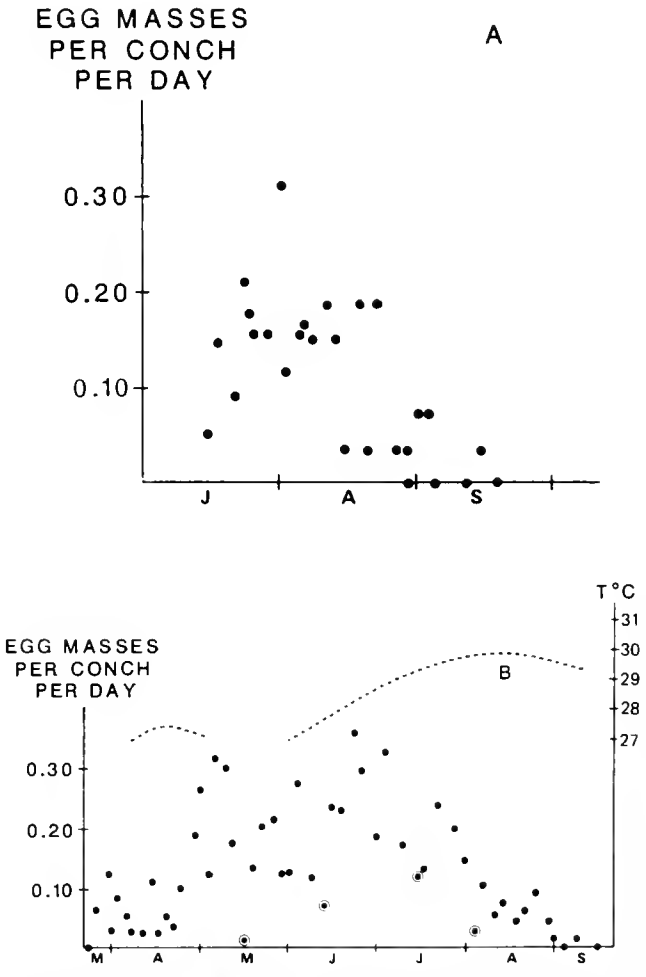


Figure 3. (A) 1981 egg-laying months, second half of the season at the egg farm; (B) 1982 egg-laying months, full season at the egg farm. Visiaul fit temperature curve (Davis and Hesse 1982).

Egg masses of 96 and 414 were recorded in 1981 and 1982, respectively. The mean number of egg masses laid per female per day in 1981 was 0.062 (n = 25; SD = 0.053) or 1.2 egg masses per female per month. The mean number of egg masses laid per female per day in 1982 was 0.041 (n = 50; SD = 0.035) or 1.7 egg masses per female per month. During the 1982 breeding season, an average of 9.4 egg masses per female were laid at the breeding site.

The number of egg masses increased from an average of 9.6 egg masses per week with 50 conchs present during the 1981 season to an average of 16.6 egg masses per week during the 1982 season with 100 to 120 conchs present. This increase in productivity was attributed to the increase in brood stock.

This work demonstrates that adult *Strombus gigas* can successfully be transferred to an enclosed breeding site. No problems of increased predation or limited food supply were observed to adversely affect conchs or the quality of the egg masses in the enclosure. These findings are important to the extent that a reliable source of healthy egg masses are necessary in mariculture of the queen conch. In 1982, the breeding site produced more than 10 egg masses per week on a continual basis for the 21-week breeding season. A supply rate of 10 egg masses per week would be adequate to support a 40-tank, commercial-scale hatchery (Davis, unpublished).

ACKNOWLEDGMENTS

The authors thank the following people and organizations for their dedication, time, and support which made this project possible: PRIDE Director Ralph Hesse, station manager Gary Hodgkins, technicians Kenneth Williams and Bertha Bell; The Griffis Foundation; The Rockerfeller Brothers Fund; Chris and Holly Dupont; and Meridian Marine Enterprises.

REFERENCES CITED

Berg, C. J., Jr. 1976. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. *Mar. Biol. (Berl.)* 34(3):191–199.

Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus* and *S. pugilus* in Los Roques, Venezuela. *Bull. Mar. Sci.* 27(4):668–680.

D'Asaro, C. N. 1965. Organogenesis, development and metamorphosis in the queen conch, *Strombus gigas*, with notes on breeding habits. *Bull. Mar. Sci.* 15(2):358–416.

Davis, M. & R. C. Hesse. 1982. Third world level conch mariculture in the Turks and Caicos Islands. *Proc. Gulf Caribb. Fish. Inst.* 35:73–82.

Fredrick, J. A. 1975. Conch research report. Peace Corps, Belize, C.A. (Available from: Belize Fisheries Unit, Box 148, Belize City, Belize)

Hesse, K. O. 1976. An ecological study of the queen conch, *Strombus gigas*. Storrs, CT: Univ. of Connecticut. 107 p. Thesis.

Randall, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas*. *Bull. Mar. Sci.* 14:246–295.

Robertson, R. 1959. Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. *Proc. Malacol. Soc. Lond.* 33(4):164–171.

Journal of Shellfish Research, Vol. 4, No. 1, 23–30, 1984.

INGESTION, ASSIMILATION, AND GROWTH OF JUVENILES OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ FED EXPERIMENTAL DIETS

LEROY CRESWELL[1]
Rosenstiel School of Marine and Atmospheric Sciences
University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149

ABSTRACT Commercial feeds and natural diets were evaluated for their acceptability by juveniles of the queen conch *Strombus gigas* Linné reared under laboratory conditions. Ingestion rates, assimilation efficiencies, and growth rates for conchs fed experimental diets were determined. Commercial artificial diets, marine angiosperms, and coarse macroalgae were not ingested by juvenile conchs. Filamentous algae [*Enteromorpha prolifera* Müller and *Spyridia filamentosa* (Wulfen)] and unicellular alga [*Spirulina platensis* (Nordst)] were readily ingested by juvenile conchs, while angiosperms (*Thalassia testudinum* König and *Syringodium filiforme* Kützing) and coarse macroalgae (*Ulva lactuca* Linnaeus and *Dictyota cervicornis* Kützing) were not consumed and did not support growth. Conchs fed *S. filamentosa* and *E. prolifera* exhibited the greatest ingestion and growth rates of diets tested. Weight-specific ingestion rates for conchs fed these diets were 11.3% and 10.3% of the conch's meat weight per day, respectively. Weight-specific ingestion rates declined with increasing conch meat weight. Assimilation efficiencies for accepted diets ranged from 56.4% (*D. cervicornis*) to 75.6% (*E. prolifera*). *Enteromorpha prolifera* and *S. filamentosa* supported the greatest growth rates of diets tested, 8.2% and 9.9% increase in meat weight over 21 days, respectively. Weight-specific ingestion rates, growth, and food-conversion ratios for selected diets are given.

KEY WORDS: queen conch, *Strombus gigas*, assimilation, growth

INTRODUCTION

The queen conch *Strombus gigas* Linné is an herbivorous gastropod inhabiting the shallow, nearshore waters of the tropical western Atlantic. It has been a target species for subsistence-level fishing throughout its range since pre-Columbian times. In recent years, this species has become a lucrative commercial commodity for resource-poor Caribbean nations, and today is the second most-valuable fishery product in the region after the spiny lobster *Panulirus argus* (Latreille) (Brownell and Stevely 1981).

Queen conch stocks have been drastically depleted in virtually every country supporting commercial export markets because of overfishing. Governments and private organizations in several conch-fishing nations have recognized the need to develop technologies for rearing conchs in hatcheries for reseeding appropriate habitats whose natural populations have been extirpated by overfishing (Berg 1981).

Brownell (1977) first successfully reared queen conch larvae through metamorphosis and discussed the mariculture potential of this species, but his culture methods and the prevailing biotic and abiotic conditions were ill-defined. Recent efforts have led to more precise documentation of conch larval biology and culture techniques (Ballantine and Chanley 1981, Siddall and Creswell 1982, Davis and Hesse 1983, Laughlin and Weil 1983). Although the technical capability to rear conchs in the laboratory has been demonstrated, the economic feasibility of conch mariculture has not yet been established. The profitability of conch mariculture will be influenced by the costs of seed production, mortality, and growth of juveniles held in high-density nursery systems, and subsequent predation and growth of seeded conchs in natural habitats. Poor survival or slow growth of juvenile conchs resulting from inappropriate or inadequate food supply during the nursery phase will prolong holding time and increase hatchery costs.

Presently, the identification and production of appropriate feeds for juvenile conchs in nursery systems are major constraints to its mariculture development. The objective of this study was to evaluate a variety of artificial and natural diets as potential foods for hatchery-reared juvenile queen conchs ranging in total shell length from 6 to 30 mm, with emphasis given to the following areas:

1. Acceptability of experimental diets;
2. Assimilation efficiency of acceptable diets, and the influence of conch stocking density and size on assimilation efficiency;
3. Wet-weight and dry-weight ingestion rates for experimental diets fed to conchs, and the influence of conch stocking density and size on ingestion rates;
4. Growth rates of juvenile conchs fed experimental diets, and the influence of conch stocking density and size on growth rate; and,
5. Food conversion efficiency of experimental diets, and the influence of conch stocking density and size on food conversion efficiency.

[1]Present address: Division of Applied Biology, Harbor Branch Foundation, Ft. Pierce, FL 33450.

MATERIALS AND METHODS

Hatchery-reared juveniles of the queen conch *Strombus gigas* were provided several artificial and natural diets to determine their food preferences (Table 1). Prior to each feeding experiment, juvenile conchs, cultured in the laboratory from a single egg mass, were cleaned and starved for 48 hours. Fecal pellets were collected every 12 hours until defecation discontinued, within 18 to 24 hours. After 72 hours, the conchs were weighed and provided a preweighed portion of food for 48 hours. Artificial pelleted diets were provided in the same form in which they were received from the manufacturers, while flaked diets and yeast were mixed with distilled water (50% by weight), extruded, and dried for 48 hours at 60°C. Natural diets were cleaned and sonicated to remove epiphytes and detritus. Each feeding trial consisted of five juvenile conchs, 6- to 30-mm shell length, placed in a 1 ℓ beaker containing 500 mℓ of 0.3 μm filtered seawater (6.1 conchs/100 cm^2 total submerged surface area). Experiments were conducted under continuous illumination, temperature was maintained at 23.5 ± 0.5°C, and culture water was exchanged daily to remove fecal material. After 48 hours the remaining food was collected, rinsed with distilled water, and weighed to ± 0.01 mg. Control experiments consisted of preweighed portions of food placed in beakers without conchs for 48 hours. A paired Student's "T" test (a = 0.05) was employed to detect gains or losses in whole wet weight of test diets fed to conchs and controls during the experimental period.

TABLE 1.

Artificial and natural diets provided to juveniles of the queen conch *Strombus gigas* in feeding and growth experiments.

Artificial Diets	Natural Diets
Pelleted Feeds	*Marine Angiosperms*
Purina marine ration Ralston Purina Co. St. Louis, Missouri	*Thalassia testudinum* König *Syringodium filiforme* Kützing
Zeigler shrimp ration Zeigler Bros., Inc. Gardners, Pennsylvania	*Marine Macroalgae* *Enteromorpha prolifera* Müller *Dictyota cervicornis* Kützing *Spyridia filamentosa* (Wulfen) *Ulva lactuca* Linnaeus
Central Soya master mix Central Soya, Inc. St. Louis, Missouri	*Marine Microalgae*
Extruded Diets	*Spirulina platensis* (Nordst)
Tetra "SMP" fish food Tetra Sales (USA) Morris Plains, New Jersey	
Extruded "torula yeast" U.S. Biochemical Co. Cleveland, Ohio	

Gross assimilation efficiency for conchs fed test diets was determined gravimetrically. Five conchs were provided a preweighed ration for 48 hours, and their fecal pellets were pipetted onto dried and preweighed filter paper (Whatman GFC) every 12 hours and dried to constant weight at 60°C. The food remaining after 48 hours was collected on a 132-μm "Nitex" screen, blotted dry, and weighed. Samples were dried to constant weight at 60°C. The conchs were starved for an additional 24 hours, and fecal pellets were collected until defecation ceased. Gross assimilation efficiency (%) was calculated from three replicated treatments as:

$$\text{dw food ingested} - \text{dw fecal pellets}/\text{dw food ingested} \times 100$$

where dw = dry weight.

Diets, which were accepted by queen conchs, were provided for 21 days to compare ingestion rates and growth of conchs among diets. Natural diets tested in the growth experiments included: (1) *Spyridia filamentosa* (Wulfen), *Enteromorpha prolifera* Müller and *Dictyota cervicornis* Kützing (macroalgae), (2) *Spirulina platensis* (Nordst) (extruded microalga), and (3) *Thalassia testudinum* König (marine angiosperm). Starved conchs served as a control group. Because artificial diets were not consumed by juvenile conchs during 48-hour experiments, they were deleted from growth experiments.

Ingestion rates were calculated as the difference between initial and final wet weights of food provided for 48 hours. Dry-weight ingestion rates were calculated from an experimentally determined wet-weight:dry-weight ratio for each diet. Ingestion rates for test diets were compared by analysis of variance (ANOVA; a = 0.05). Weight-specific ingestion rates were calculated as the weight of food consumed and expressed as a percentage of conch's live-meat weight. Live-meat weight for each conch was calculated from the following whole weight–meat weight regression derived from sibling juvenile conchs:

$$\text{wet meat weight (mg)} = 19.19 + (0.3998)\,\text{whole wet weight (mg)}$$

where N = 40 and $r^2 = 0.9763$.

Growth of conchs fed experimental diets was measured as the increase in meat weight over 21 days. Weight-specific growth was defined as the increase in meat weight of conchs, expressed as a percentage of their initial meat weight, over this period. Food conversion ratios (FCR) were calculated from replicate trials for each test diet using the following equation:

$$\text{dw food ingested (mg)}/\text{ww meat increase (mg)} = \text{FCR}$$

where ww = wet weight.

The influence of conch-stocking density on ingestion rate, assimilation efficiency, growth, and food conversion was tested for juveniles fed *E. prolifera*, a preferred diet. Fifteen conchs held individually in 1 ℓ beakers (1.2 conchs/100 cm^2 bottom surface area) were provided preweighed portions of this alga. These experiments were conducted concurrently and under the same conditions as conchs held at high density (6.1 conchs/100 cm^2) and fed the same diet. The effect of conch stocking density on ingestion rate, assimilation efficiency and growth were compared by ANOVA ($a = 0.05$). Proportional values, such as assimilation efficiency, weight-specific ingestion rate and growth, were arcsine-transformed for statistical analysis.

The influence of conch size on ingestion rate, assimilation efficiency and growth was evaluated for the 15 conchs held individually and fed *E. prolifera* in the experiment described above. The whole weight of conchs in this experiment ranged from 75 to 1,458 mg. The influence of conch weight on these parameters was evaluated by regression analysis.

RESULTS AND DISCUSSION

No artificial diets tested in this study were accepted by juvenile queen conchs. Conchs were not observed feeding nor did they produce fecal pellets during the 48 hours these diets were available. The instability of pelleted and extruded diets in seawater precluded weight measurements after soaking. Ballantine and Chanley (1981) reported that a variety of pelleted feeds, including *Tilapia* ration, rabbit and chicken feeds, were not accepted by juvenile conchs.

Marine angiosperms, *Thalassia testudinum* and *Syringodium filiforme* Kützing, and the coarse green macroalga, *Ulva lactuca* Linnaeus, also were not ingested by juvenile conchs (Table 2). Although *S. filiforme* and *U. lactuca* were deleted from 21-day growth experiments, *T. testudinum* was provided to conchs for 21 days. It was not ingested at any time during this period.

Dictiyota cervicornis, *Enteromorpha prolifera*, *Spyridia filamentosa* and *Spirulina platensis* were acceptable diets for juvenile conchs (Table 3). *Enteromorpha prolifera* and *S. filamentosa* were consumed in greater quantities than other diets ($a = 0.001$). A Student-Newman-Kuels (SNK) multiple-range test among the diets ranked the mean weight-specific ingestion rates (wet weight of food consumed per 48 hours as a percentage of conch live-meat weight) in the following order ($a = 0.05$):

D. cervicornis	*S. platensis*	*E. prolifera*	*S. filamentosa.*
6.4%	19.5%	20.6%	22.6%

Dry-weight ingestion, calculated from a wet weight–dry weight relationship for each diet, magnified the disparity between ingestion rates. Weight-specific ingestion (dry weight/48 hours) of *S. filamentosa* and *E. prolifera* were highest among the test diets:

D. cervicornis	*S. platensis*	*E. prolifera*	*S. filamentosa.*
0.9%	2.6%	4.0%	4.0%

Ingestion rates declined at higher stocking density ($P = 0.002$; Table 4). Fifteen conchs in the high-density treatment (6.1 conchs/100 cm^2), feeding on *E. prolifera*, ingested 20.6 ± 1.1% of their live-meat weight in 48 hours, while conchs stocked at low density consumed 31.8 ± 2.5% of their meat weight. Dry-weight ingestion of *E. prolifera* per 48 hours was 4.0 ± 0.3% and 6.3 ± 0.4% of the initial conch meat weight when held at high and low density, respectively.

Total consumption of *E. prolifera* increased with increasing conch size (Figure 1). Although food consumption was higher for larger conchs, weight-specific ingestion rates declined with increasing conch meat weight. The decrease in weight-specific ingestion rates was linearly proportional to the conch's meat weight (Figure 2).

Ingestion rates for conchs in this study were similar to those reported for other herbivorous gastropods. Koike et al. (1979) reported that daily weight-specific feeding rates for the ormer or tuberculate abalone *Haliotis tuberculata* Linné ranged from 1.8% for *Rhodymenia* sp. to 4.4% for mixed macroalgae (dry-weight food). Daily consumption rates for pinto abalone *Haliotis kamtschatkana* Jonas feeding on fresh *Undaria* sp. ranged from 5% to 2% of the abalone's meat weight, with weight-specific ingestion declining with increasing meat weight (Paul et al. 1977). Grahame (1973) observed that the common periwinkle *Littorina littorea* Linné consumed 2.83% of its meat weight per day while feeding on *Ulva lactuca* (dry-weight food). The terrestrial pulmonate *Agriolax reticulatus* Müeller consumed 14% (wet-weight food) of its body weight per day while feeding on leaves and other plant matter (Pallant 1975). The woodland snail *Oxychilus celliarus* (Müller) consumed 1.25% (dry-weight food) of its meat weight per day while feeding on lettuce (Mason 1970).

The type of algal diet exerted a significant influence on the assimilation efficiency of juvenile conchs ($P = 0.001$). *Enteromorpha prolifera* and *S. filamentosa* were assimilated more efficiently than other diets tested (Table 5). An SNK multiple-range test ranked assimilation efficiency for these diets in the following subsets that were significantly different at the $a = 0.05$ level:

D. cervicornis	*S. platensis*	*S. filamentosa*	*E. prolifera.*
56.4%	67.4%	72.6%	75.6%

In this study, the observed assimilation efficiencies for *Strombus gigas* are similar to those reported for other

TABLE 2.

Initial and final wet weights of experimental diets provided to juveniles of the queen conch *Strombus gigas* and control diets for 48 hours. Where controls indicated a significant change in wet weight, percent weight change was compared to test diets by analysis of variance (ANOVA; a = 0.05).

Diet	Initial Wet Weight (mg)	Final Wet Weight (mg)	Final – Initial Wet Weight (mg)	Student's "T"	d.f.	P
Dictyota	167.5 ± 30.5	131.8 ± 25.2	– 35.7 ± 5.3	7.61	2	0.022*
Control	135.4 ± 5.9	135.2 ± 5.6	– 0.2 ± 0.6	0.13	5	0.820
Enteromorpha	485.2 ± 40.5	191.6 ± 64.2	–293.7 ± 41.1	7.14	2	0.019*
Control	86.3 ± 2.4	86.9 ± 2.3	0.5 ± 0.6	– 0.38	5	0.721
Spyridia	883.5 ± 31.3	368.9 ± 51.3	–514.6 ± 47.6	10.82	2	0.008**
Control	120.6 ± 14.5	119.5 ± 13.4	1.1 ± 2.0	0.53	5	0.621
Spirulina†	36.3 ± 3.9	15.9 ± 2.8	– 20.5 ± 4.1	5.04	2	0.037*
Control	60.6 ± 2.3	62.5 ± 2.9	1.9 ± 0.4	– 2.20	5	0.089
Thalassia‡	69.1 ± 6.5	74.2 ± 7.7	5.1 ± 2.3	– 3.19	23	0.007**
Control	120.6 ± 14.5	122.8 ± 14.7	2.2 ± 0.5	– 4.61	5	0.006**
Ulva‡	55.6 ± 11.8	68.1 ± 10.7	12.5 ± 7.2	– 3.62	2	0.025*
Control	148.9 ± 10.9	170.0 ± 12.2	21.2 ± 3.8	– 5.54	5	0.003**
Syringodium‡	59.1 ± 6.5	62.4 ± 6.8	3.3 ± 1.2	– 2.62	2	0.047*
Control	56.3 ± 14.3	69.1 ± 15.7	12.8 ± 2.1	– 5.96	5	0.027*

*Significant

**Highly significant

†Values given for *Spirulina* are dry weights

‡Wet weight increased significantly for both experimental and control diets. One-way analysis of variance indicated no difference between percent weight changes between experimental and control samples.

Thalassia: F = 0.009; d.f. = 1, 27; P = 0.924

Ulva: F = 1.075; d.f. = 1, 6; P = 0.334

Syringodium: F = 1.146; d.f. = 1, 6; P = 0.299

TABLE 3.

Wet weight, dry weight, and weight-specific ingestion rates for experimental diets fed to juveniles of the queen conch *Strombus gigas* for 21 days.

Diet	Wet Weight Food Ingested/48 Hours (mg)	Wet Weight Ingested (% meat weight)	Dry Weight Food Ingested/48 Hours (mg)	Dry Weight Ingested (% meat weight)
Dictyota	188.2 ± 24.5	6.4 ± 0.8	22.8 ± 2.6	0.9 ± 0.01
Enteromorpha	853.7 ± 46.1	10.6 ± 1.1	168.4 ± 8.9	4.0 ± 0.3
Spyridia	665.8 ± 52.7	22.6 ± 1.9	119.7 ± 9.1	4.0 ± 0.3
Spirulina	620.8 ± 69.6	19.5 ± 2.3	82.7 ± 7.0	2.6 ± 0.2
Thalassia		Not consumed		
One-way analysis of variance	F = 30.6 d.f. = 3, 36 P = 0.001	F = 27.7 d.f. = 3,36 P = 0.001	F = 69.0 d.f. = 3, 36 P = 0.001	F - 67.1 d.f. = 3,36 P = 0.001

TABLE 4.

The influence of stocking density on ingestion, assimilation efficiency, growth rate, and food conversion efficiency of juveniles of the queen conch *Strombus gigas* fed *Enteromorpha prolifera* for 21 days.

	Low Density (1.2 conchs/100 cm^2)	High Density (6.1 conchs/100 cm^2)	One-Way Analysis of Variance
Initial meat weight (mg)	211.9 ± 44.7	275.4 ± 34.5	F = 2.251 d.f. = 1, 29 P = 0.1451
Wet weight ingested/48 hours (mg)	1017.3 ± 76.6	853.6 ± 46.1	F = 3.352 d.f. = 1, 19 P = 0.0837
Weight-specific ingestion/48 hours (wet weight) (mg)	31.8 ± 2.5	20.6 ± 1.1	F = 19.020 d.f. = 1, 19 P = 0.0004
Dry weight ingested/48 hours (mg)	200.2 ± 14.9	168.4 ± 8.9	F = 3.358 d.f. = 1, 19 P = 0.0835
Weight-specific ingestion/48 hours (dry weight) (%)	6.3 ± 0.4	4.0 ± 0.3	F = 21.616 d.f. = 1,19 P = 0.0002
Assimilation efficiency (%)	69.4 ± 1.8	76.2 ± 1.0	F = 3.400 d.f. = 1, 17 P = 0.0838
Weight-specific growth/21 days (% meat weight)	24.7 ± 0.9	8.2 ± 0.5	F = 225.9 d.f. = 1, 29 P = 0.001
Food conversion ratio	3.1 ± 0.2	5.3 ± 0.3	F = 24.668 d.f. = 1, 19 P = 0.001

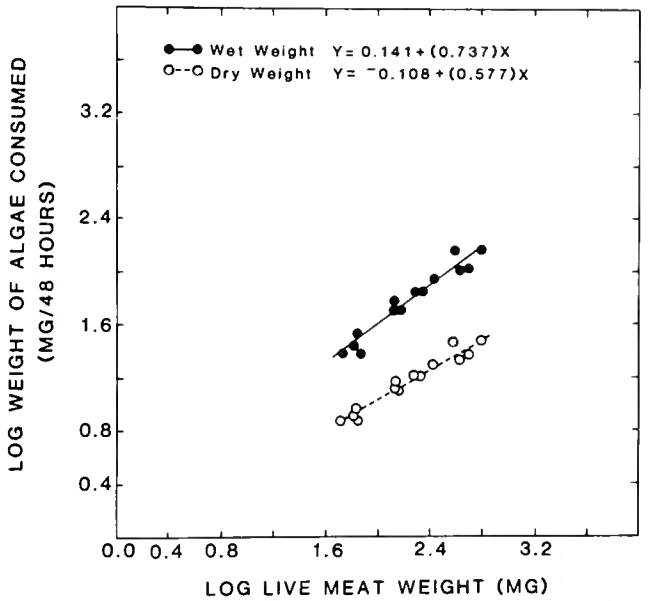


Figure 1. Wet- and dry-weight ingestion of *Enteromorpha prolifera* fed to juveniles of the queen conch *Strombus gigas* for 21 days.

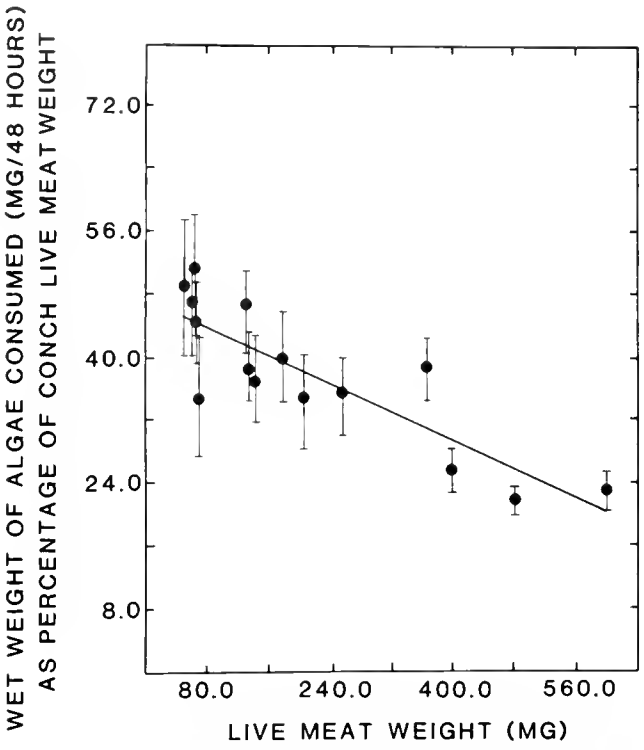


Figure 2. Weight-specific ingestion rates for juveniles of the queen conch *Strombus gigas* fed *Enteromorpha prolifera* for 21 days. Ingestion rates are expressed as the weight of algae consumed as a percentage of the conch's meat weight per 48 hours. Percent wet weight of algae consumed = 47.60 – (0.0452) conch meat weight ($N = 15; r^2 = 0.7363$).

herbivorous gastropods. The grey field slug *Agriolax reticulatus* assimilated 77% of ingested carrots and leafy plant matter (Pallant 1975). Stern (1969) noted that the pulmonate *Arion rufus* (Linné) assimilated 74% of the lettuce it ingested. Similarly, the woodland snail *Oxychilus celliarus* was found to assimilate 70.2% of ingested lettuce (Mason 1970).

Preferred diets were assimilated more efficiently than less attractive foods. Carefoot (1967) reported a similar relationship between ingestion and assimilation for the seahare *Aplysia punctata* Cuvier. This opisthobranch assimilated preferred diets (*U. lactuca, Cryptopleura ramosa* Abbott, *Heterosiphonia plumosa* (Ellis), and *Plocamium coccineum* Lamour) more efficiently than algae marginally ingested. Assimilation of those diets ranged from 75% to 65% (in the order given), while coarse diets, such as *Delessaria sanguina* (Huds.) and *Laminaria digitata* (Huds.) were ingested in smaller quantities and were assimilated less efficiently (45% and 53%, respectively).

Assimilation efficiency was not influenced by conch stocking density. Conchs maintained at high density assimilated 67.4 ± 1.4% of ingested cells of *S. platensis*, while conchs in the low density treatment assimilated 68.4 ± 1.9%. Similarly, conchs fed *E. prolifera* assimilated 76.2 ± 1.0% and 69.8 ± 1.8% of this diet at high and low conch densities, respectively (Table 4). Assimilation efficiency was not affected by conch size for the above diets. Throughout the size range tested, there was no significant difference in assimilation efficiency of these diets with respect to conch meat weight.

TABLE 5.

Assimilation efficiency of juveniles of the queen conch *Strombus gigas* fed experimental diets for 48 hours. Each trial consisted of five conchs stocked at 6.1 conchs/100 cm^2.

Diet	Trial	Dry Weight of Food Ingested (mg)	Dry Weight of Fecal Pellets (mg)	Assimilation Efficiency (%)
Dictyota	1	5.89	2.33	60.4
	2	7.59	3.48	54.2
	3	6.07	2.76	54.5
	$\bar{x} \pm$ SE*			56.4 ± 2.0
Enteromorpha	1	75.81	15.39	79.7
	2	50.17	12.45	75.2
	3	53.88	15.02	72.1
	$\bar{x} \pm$ SE			76.2 ± 2.2
Spyridia	1	31.27	9.99	68.1
	2	16.23	4.60	71.1
	3	26.44	6.22	76.5
	$\bar{x} \pm$ SE			72.8 ± 2.4
Spirulina	1	26.29	9.18	65.1
	2	25.02	8.26	67.2
	3	30.42	9.16	69.9
	$\bar{x} \pm$ SE			67.4 ± 1.4
One-way analysis of variance of diet on assimilation efficiency				F = 21.61 d.f. = 3, 8 P = 0.0003

*standard error

Conchs fed *D. cervicornis, S. platensis, S. filamentosa* and *E. prolifera* increased in meat weight over 21 days, while starved conchs and those provided with *T. testudinum* declined in meat weight (Table 6). An SNK multiple-range test ranked weight-specific change in meat weight for conchs fed experimental diets into the following significantly different subsets (a = 0.05):

Starved	*Thalassia*	*Dictyota*
−2.6%	−1.7%	2.1%

Spirulina	*Spyridia*	*Enteromorpha*
5.2%	9.9%	8.2%

TABLE 6.

Growth of juveniles of the queen conch *Strombus gigas* fed experimental diets for 21 days. Initial meat weights and changes in meat weight were compared for experimental diets by one-way analysis of variance (ANOVA; a = 0.05).

Diet	Initial Meat Weight (mg)	Final Meat Weight (mg)	Meat Weight Change (mg)	Student's "T"	d.f.	P
Dictyota	189.3 ± 20.4	196.1 ± 21.6	6.8 ± 1.8	−3.79	14	0.002
Enteromorpha	275.4 ± 34.5	299.0 ± 38.1	23.7 ± 4.0	−5.86	14	0.001
Spyridia	194.2 ± 32.3	217.7 ± 36.7	22.6 ± 5.1	−4.45	14	0.001
Spirulina	207.6 ± 33.3	221.7 ± 36.5	14.1 ± 3.6	−3.95	14	0.001
Thalassia	245.1 ± 30.3	240.6 ± 29.8	− 4.5 ± 0.9	4.80	14	0.001
Control	246.9 ± 32.3	241.0 ± 23.5	− 5.9 ± 1.1	5.20	14	0.001
One-way analysis of variance of diet on initial meat weight	F = 1.359 d.f. = 5, 89 P = 0.2482	One-way analysis of variance of diet on meat weight change	F = 17.274 d.f. = 5, 89 P = 0.001			

Weight-specific growth rates for conchs fed *E. prolifera* were not influenced by conch size. Regression analysis for the influence of meat weight on growth rate of conchs fed *E. prolifera* indicated that small conchs exhibited similar weight-specific growth rates as larger individuals.

Growth rates were significantly higher for conchs maintained at low-stocking density (Table 4). Conchs fed *E. prolifera* and maintained at high density gained 23.7 ± 4.0 mg or 8.3% of their initial meat weight in 21 days, while conchs at low density increased in meat weight by 51.9 ± 10.0 mg or 24.0% of their initial meat weight. Koike et al. (1979) noted a decline in growth of *Haliotis tuberculata* at stocking densities in excess of 2,500/m^2. Similarly, Laughlin and Weil (1983) observed a decline in growth of juvenile conchs at high-stocking densities despite *ad libitum* feeding of several algal diets.

Competition for food or agonistic behavior may be factors affecting density-dependent growth rates of juvenile conchs. Siddall (1984) reported that conchs held at high density were more active and secreted copious amounts of mucus compared to those at low-stocking density. In this study, escape responses similar to those reported for other strombids (Berg 1974, 1975) were more pronounced for conchs held at high density. Because feeding rates declined at high-stocking density, despite excess food availability, it is likely that depressed ingestion and growth rates may be attributed to a heightened interaction between conchs and the energetic losses associated with this behavior.

Food conversion ratios (FCR) varied significantly among test diets (P = 0.002, Table 7); the highest food-conversion efficiency was achieved with *D. cervicornis*. An SNK multiple-range test ranked FCR values for diets into significantly different subsets (a = 0.05) in the following manner:

D. cervicornis	*S. platensis*	*S. filamentosa*	*E. prolifera*
2.1	4.3	3.5	5.3

TABLE 7.

Food conversion ratios (FCR) for juveniles of the queen conch *Strombus gigas* fed experimental diets for 21 days. Total dry weight ingestion and meat weight gained for replicate trials of five conchs stocked at 6.1 conchs/100 cm^2 are given.

Diet	Trial	Meat Weight Gained (mg)	Dry Weight Ingested (mg)	Food Conversion Ratio
Dictyota	1	39.8	71.2	1.8
	2	26.5	64.8	2.4
	3	35.7	73.4	2.1
	$\bar{x}$ ±SE*			2.1 ±0.2
Enteromorpha	1	89.4	528.6	5.9
	2	116.1	557.8	4.8
	3	111.7	478.1	5.2
	$\bar{x}$ ±SE			5.3 ±0.3
Spyridia	1	102.7	415.4	4.0
	2	121.2	353.1	2.9
	3	105.2	387.1	3.7
	$\bar{x}$ ±SE			3.5 ±0.3
Spirulina	1	71.0	277.5	3.9
	2	50.3	278.9	5.5
	3	79.4	294.8	3.7
	$\bar{x}$ ±SE			4.3 ± 1.0
One-way analysis of variance of diet on food conversion ratio				F = 13.03 d.f. = 3, 11 P = 0.002

*standard error

Although FCR values were lowest for *D. cervicornis*, indicating higher food-conversion efficiency, ingestion rates and growth of conchs fed this alga were marginal. Carefoot (1967) observed a similar decline in food-conversion ratios for nonpreferred diets fed to *Aplysia punctata*. He suggested two possible explanations: (1) gravimetric measurements for ingestion and growth may be unreliable when ingestion and weight gain are marginal, and (2)

metabolism of partially starved animals may be lower so that fewer calories are expended for maintenance metabolism. Because 60% of the total weight of *S. gigas* is calcareous shell, weight gain observed for partially starved conchs may be attributed to shell deposition without any significant increase in meat weight, causing erroneous food-conversion ratios.

Food-conversion efficiency was enhanced at low density for conchs fed *E. prolifera*. Food-conversion ratios declined from 5.3 to 3.1, high density and low density, respectively (Table 4). Food conversion also improved with increasing meat weight for conchs fed this alga ($P = 0.001$; Figure 3).

This study suggests that commercially available, artificial diets, marine angiosperms and coarse macroalgae are inappropriate foods for juvenile queen conchs. Fresh filamentous macroalgae and extruded microalgae hold promise as potential feeds for conchs in nursery systems. Feeding rates and conversion ratios of juvenile conchs fed acceptable diets are similar to other herbivorous gastropods. Artificial diets containing homogenized fresh or dried macroalgae and other vegetable matter which are prepared in seawater-stable binders warrant further study.

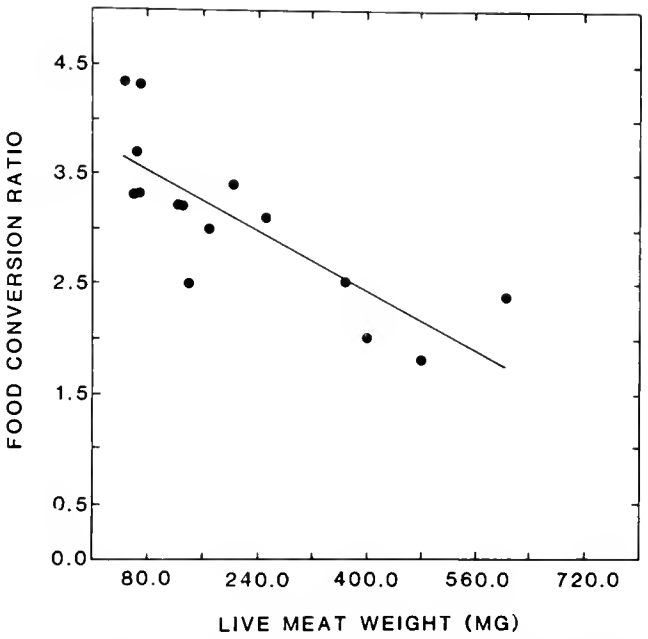


Figure 3. Food-conversion ratios (FCR) for juveniles of the queen conch *Strombus gigas* fed *Enteromorpha prolifera* for 21 days. FCR = 3.787 − (0.0034) conch meat weight ($N = 15$; $P = 0.05$).

ACKNOWLEDGMENTS

The author expresses his gratitude to Drs. Edwin Iversen, Jeffrey Prince, and Scott Siddall for their comments and suggestions during the course of this research. Special thanks to Lisa Fitzgerald and Jeff Erickson for their tireless efforts to culture queen conch larvae subsequently used in this study. This investigation was supported, in part, by the Wallace Groves Aquaculture Foundation, Freeport, Bahamas.

REFERENCES CITED

Ballantine, D. & P. Chanley. 1981. Hatchery culture and reseeding of queen conch, *Strombus gigas*, in Puerto Rico. Annual report FSE 43–81–126–18 submitted to U.S. Dept. Int., National Marine Fisheries Service. 20 pp. (Available from: Dept. of Marine Science, Univ. of Puerto Rico, Mayaguez, PR)

Berg, C. J., Jr. 1974. A comparative ethological study of strombid gastropods. *Behaviour* 51:274–322.

_____ . 1975. Behaviour and ecology of conch (Superfamily Strombacea) on a deep subtidal algal plain. *Bull. Mar. Sci.* 25: 307–317.

_____ (editor). 1981. The mariculture and fisheries management of the queen conch, *S. gigas*. Proceedings of a workshop held at the Wallace Groves Aquaculture Foundation; 1981 January 10; Freeport, Bahamas.

Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and *S. pugilus* in Los Roques, Venezuela. *Bull. Mar. Sci.* 27:668–680.

_____ & J. Stevely. 1981. The biology, fisheries and management of the queen conch, *Strombus gigas*. *U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 43(7):1–12.

Carefoot, T. H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. Mar. Biol. Assoc. U.K.* 47(3):565–589.

Davis, M. & C. Hesse. 1983. Third world level conch mariculture in the Turks and Caicos Islands. *Proc. Gulf Caribb. Fish. Inst.* 35th Ann. Meet.: 73–82.

Grahame, J. 1973. Assimilation efficiency of *Littorina littorea* (L.) (Gastropoda: Prosobranchia). *J. Ecol.* 42(2):383–390.

Koike, Yasuyuki, J. P. Flassch & J. Mazurier. 1979. Biological and ecological studies on the propagation of the Ormer, *Haliotis tuberculata* Linnaeus. II. Influence of food and density on the growth of juveniles. *Bull. Soc. Franco-Japan. Oceanogr.* Tome 17(1):43–52.

Laughlin, R. A. & E. M. Weil. 1983. Queen conch mariculture and restoration in the archipelago de Los Roques: Preliminary results. *Proc. Gulf Caribb. Fish. Inst.* 35th Ann. Meet.: 64–73.

Mason, C. F. 1970. Food, feeding rates and assimilation in woodland snails. *Oecologia (Berl.)* 4:358–373.

Pallant, D. 1975. Assimilation in the grey field slug, *Agriolax reticulatus* (Mueller). *Proc. Malacol. Soc. Lond.* 41(2):99–107.

Paul, A. M., J. M. Paul, D. W. Hood & R. A. Neve. 1977. Observation on food preferences, daily ration requirements and growth of *Haliotis kamtschatkama* (Jonas) in captivity. *Veliger* 19(3):303–309.

Siddall, S. E. 1984. Density-dependent levels of activity of juveniles of the queen conchs *Strombus gigas* Linné. *J. Shellfish Res.* 4(1): 67–74.

_____ & R. L. Creswell. 1982. High density hatchery production of juveniles of the queen conch *Strombus gigas* L. *J. Shellfish Res.* 2(1):107 (Abstract).

Stern, G. 1969. Bilan energetique de la limace *Arion rufus* (Mollusque Pulmone) en periode de croissance. *C. R. Herd. Seances Acad. Sci.* 269:1015–1018.

Journal of Shellfish Research, Vol. 4, No. 1, 31–35, 1984.

SUBLETHAL EFFECTS OF COPPER ON JUVENILES OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ

ILSE M. SANDERS
Center for Energy and Environment Research
University of Puerto Rico
Marine Ecology Division, College Station
Mayaguez, Puerto Rico 00708

ABSTRACT Juveniles of *Strombus gigas* Linné (27 to 62 mm shell length) were exposed to sublethal concentrations of copper. Grazing rates, growth rates, fecal pellet production and righting time were evaluated as physiological and behavioral responses for possible use as indicators of sublethal stress from exposure to dissolved copper. Sublethal, static, 27-day bioassays were performed at 30 and 60 $\mu g \cdot \ell^{-1}$ total copper; flow-through, 7-day bioassays were performed at 340 $\mu g \cdot \ell^{-1}$ total copper. Significant reductions in grazing rates and fecal pellet production were detected for conchs that were exposed to copper. Grazing rates and fecal pellet production showed a significant positive correlation. Righting time was longer for conchs exposed to copper and its measurement is suggested as a means of quantifying sublethal effects.

KEY WORDS: *Strombus gigas*, copper toxicity, physiology, behavior

INTRODUCTION

Among the criteria used to evaluate the potential impact of heavy metals on marine organisms is the lethal concentration which kills 50% (LC_{50}) of an exposed group of organisms (Sprague 1969). Such tests are used to predict "safe" limits for discharges of toxicants to marine waters. These tests do not take into consideration many possible sublethal effects that these toxicants may induce in natural populations (Sprague 1976, Ahsanullah et al. 1981). Sublethal bioassays can be conducted using ecologically relevant factors such as feeding, growth, and reproduction. The effects of sublethal concentrations of copper, zinc, and nickel on physiological and behavioral processes of marine organisms have been demonstrated (Timourian and Watchmaker 1972, Reeve et al. 1977, D'Silva and Kureishy 1978, Davenport and Manley 1978, Moraitou-Apostolopoulou and Verriopoulos 1979, Kumaraguru et al. 1980, Sullivan et al. 1983), and those processes are more appropriate to predict the effect of chronic, low-level concentrations of these metals on marine organisms.

Copper, an essential trace metal for both freshwater and marine organisms, can also become, at increased concentrations, one of the most highly toxic metals in the aquatic environment. In marine molluscs, 96-hour LC_{50} levels have been reported at concentrations of 20 to 1,000 $\mu g \cdot \ell^{-1}$ total copper (Nriagu 1979). Lower copper concentrations may be indirectly lethal if they adversely alter normal behavioral and physiological responses of organisms. As a result of river drainage through geological deposits of copper, background levels for metals in nearshore water and sediments are elevated along the western coast of Puerto Rico: 6 $\mu g \cdot \ell^{-1}$ particulate, 8 $\mu g \cdot \ell^{-1}$ soluble total copper (Lowman et al. 1966, Montgomery and Santiago 1978). Industrial discharges could increase these concentrations thereby threatening important coastal environments, such as seagrass beds.

The purpose of this study was to evaluate several physiological and behavioral responses of juveniles of the queen conch *Strombus gigas* Linné for use as indicators of sublethal effects of copper. The responses studied were grazing and growth rates, fecal pellet production, and righting time.

MATERIALS AND METHODS

Test solutions were prepared from a stock solution of reagent-grade $CuCl_2$ (anhydrous) in seawater. Stock solutions were mixed daily and ranged from 6,000 to 9,000 $\mu g \cdot \ell^{-1}$ total copper. Appropriate aliquots of stock solution were added to test chambers by means of pipettes (static bioassays) or a peristaltic pump (flow-through bioassay). The required quantity of total copper was extracted and mixed with seawater to form the desired test concentrations. No changes in background levels of pH or salinity were detected at final dilutions. In test chambers, salinity ranged from 35.5 to 36.5 ppt and pH ranged from 7.8 to 8.1.

Total initial copper in stock and test solutions was analyzed using a Perkin-Elmer Model 2380 atomic absorption spectrophotometer. Seawater was used to prepare the standards that were, in turn, used to quantify the copper of the test samples. Replicate samples were analyzed for each concentration tested. The speciation of copper within the system was not determined.

Laboratory-reared conch juveniles were obtained from the University of Puerto Rico, Department of Marine Sciences. They ranged from 26.8 to 61.6 mm in shell length. They were maintained in flow-through aquaria at the Center for Energy and Environment Research laboratories.

Two kinds of sublethal copper bioassays were performed between January and April 1982 with juvenile conchs: a static system in which growth and grazing were determined

during 27 days, and a flow-through system in which grazing rates, fecal pellet production, and righting time were determined.

Static bioassays were conducted in crystallizing dishes (125 × 64 mm) with one conch per plate for a total of 15 per concentration and control. Tests were performed at two different concentrations: 30 and 60 $\mu g \cdot \ell^{-1}$ total copper at 25 ± 1°C. Solutions were exchanged every 48 to 72 hours.

The flow-through bioassays were conducted with eight copper-exposed and seven control conchs in two shallow tanks (11 × 76 × 113 cm) with a volume of about 95 ℓ. Solutions were maintained at 340 $\mu g \cdot \ell^{-1}$ total copper by means of peristaltic pumps. In the tank, individual conchs were isolated within boxes (15 × 10.8 × 7.2 cm) which were perforated on the sides and top, and covered with Nitex® mesh (mesh size: 1,000 μ) to allow for water exchange and minimize algae or fecal pellets loss. Temperature was maintained at 27 ± 1°C.

Conchs were fed *Spyridia filamentosa* (Wulfen), a preferred food, during holding and exposures (Appeldoorn et al. 1983). Every 48 to 72 hours the unconsumed algae were removed and a new quantity added. Algae were weighed immediately before and after exchanges. Grazing rates were expressed as the wet weight of algae consumed (μg) per conch wet weight (mg) per 24 hours. Originally, only shell lengths of the conchs were determined. A regression equation [$\log y = -9.4069 + 2.9301(x)$, $r = 0.98$, $n = 30$] was calculated using similar size conchs to convert length into weight. During the static bioassay, shell length was measured from the apex of the shell to the spire every seven days and growth was expressed as the difference between initial and final size per day.

Fecal pellets were collected by carefully washing out the contents of each box every 48 hours. The water containing fecal pellets was filtered through previously weighed filter paper (GF/C: Whatman). The residue was dried at 60°C for 24 hours and cooled in a desiccator for 6 hours. Fecal pellets production was expressed as dry weight (μg) per conch wet weight (mg) per 24 hours.

Strombids right themselves with a kicking motion of the operculum which is attached to the posterior portion of the foot (Randall 1964, Berg 1975). The time (up to 180 seconds) required for conchs to right themselves when overturned was measured twice for experimental animals exposed to 340 $\mu g \cdot \ell^{-1}$ total copper and twice for the control conchs.

Acute mortality, flow-through, 96-hour bioassays were conducted at 400 and 1,100 $\mu g \cdot \ell^{-1}$ of total copper by the method recommended by the American Society for Testing and Materials (ASTM 1980). Fifteen animals per concentration and control were used. The criterion for mortality was failure to respond to stimulation with a probe. The statistical tests used are described in Sokal and Rohlf (1981).

RESULTS

Exposures of *Strombus gigas* to 30 and 60 $\mu g \cdot \ell^{-1}$ total copper during 27 days in a static bioassay system resulted in a significant difference between the grazing rates of organisms exposed and those of the control (Kruskal-Wallis, $p < 0.05$). Figure 1 illustrates the results. The grand mean grazing rates (algal wet weight per conch wet weight per day) were 0.051, 0.053, and 0.057 mg $\cdot$ mg^{-1} $\cdot$ day^{-1}, respectively, for 60, 30, and 0 (control) $\mu g \cdot \ell^{-1}$ total copper.

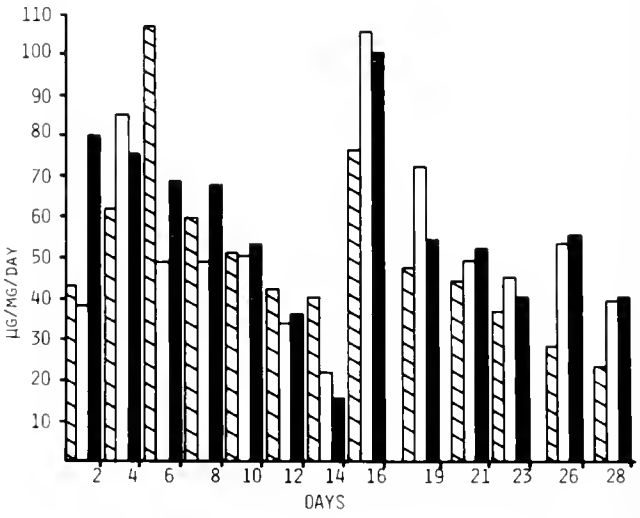


Figure 1. Grazing rates of conchs exposed to 60 (striped bars), 30 (solid bars), and 0 (clear bars) $\mu g \cdot \ell^{-1}$ total copper.

Growth in conchs of 27- to 36-mm shell length was not detectably affected by these exposures. Mean growth rates were 0.12 ± 0.03 SD, 0.11 ± 0.02 SD, and 0.13 ± 0.04 SD mm $\cdot$ day^{-1} for total copper exposures of 60, 30, and 0 (control) $\mu g \cdot \ell^{-1}$, respectively.

In the flow-through bioassay, exposure to higher concentrations of copper resulted in an immediate cessation of grazing in some animals (Figure 2). The average consumption of algae was reduced by over 90% by a 48-hour exposure to 340 $\mu g \cdot \ell^{-1}$ of total copper. Control animals consumed an average of 111 $\mu g \cdot mg^{-1} \cdot day^{-1}$, while treated animals grazed only 10 $\mu g \cdot mg^{-1} \cdot day^{-1}$. These differences in grazing rates were significant (Mann-Whitney U-Test, $p < 0.01$). Although there was an indication of a decline in feeding with time, all control animals consumed algae throughout the entire experiment.

The rates of fecal pellet production among conchs exposed to 30 $\mu g \cdot \ell^{-1}$ of total copper were always lower than those of control conchs (Mann-Whitney U-Test, $p < 0.01$) (Figure 2). As previously observed for grazing rates, an immediate reduction in the rate of fecal pellet production was observed during the first 48 hours, and this reduction continued throughout the experiment.

The reduction of grazing and fecal pellet production rates followed the same trend throughout the experiment.

A significant, positive-correlation coefficient of 0.4 ($p \geq 0.01$) was found between these two parameters using the Kendall test.

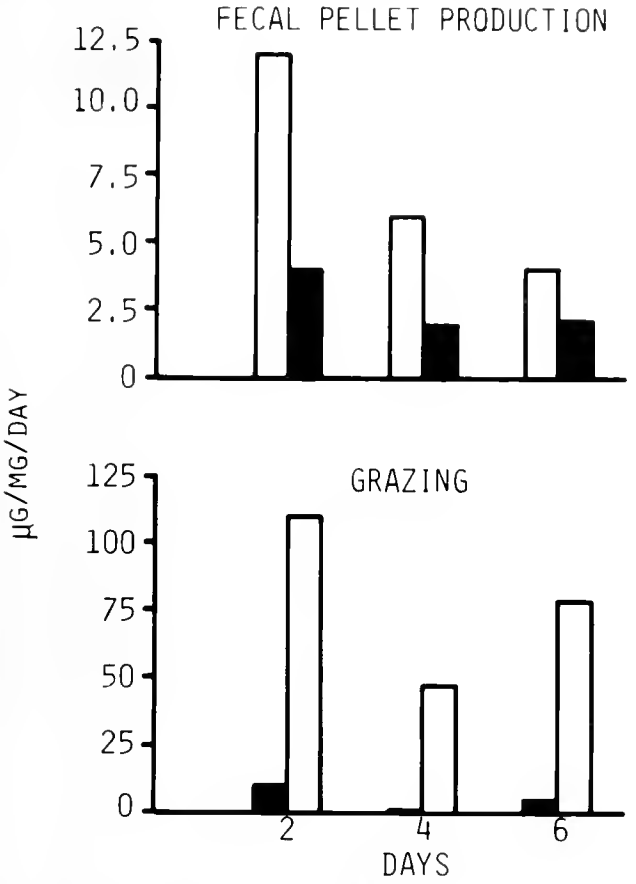


Figure 2. Fecal pellet production and grazing of conchs exposed to 340 (solid bars) and 0 (clear bars) $\mu g \cdot \ell^{-1}$.

During two trial periods the mean righting response time for the control conchs was 54 seconds. Test animals, which were exposed to 340 $\mu g \cdot \ell^{-1}$ of total copper, had a mean righting response of 100 seconds by comparison. Two copper-exposed conchs were unable to right themselves during the second standard 3-minute trial period.

Conchs were exposed to higher concentrations of copper in a 96-hour toxicity test to develop a basis for comparing sublethal with lethal measures. Table 1 shows percent mortality of conchs exposed to 400 and 1,100 $\mu g \cdot \ell^{-1}$ of total copper for a period of 96 hours.

DISCUSSION

Copper concentrations were measured and reported as total copper in accordance with recent literature pertaining to copper toxicity in marine organisms (e.g., Steele 1983, Sullivan et al. 1983) and with reporting standards of the U.S. Environmental Protection Agency. Studies have demonstrated, however, that metal toxicity to a number of marine organisms is related to metal ion activity rather than to total metal concentration (Sunda and Guillard 1976, Engel and Sunda 1979). Accumulation of copper is also related to cupric ion activity irrespective of the total concentration of copper or chelating agents present (Zamuda and Sunda 1982).

Measurement of copper speciation in seawater is difficult because of low total metal concentration and high ability of the metal to form complex molecules with other ions (Sunda and Ferguson 1983). Synthetic chelators, such as EDTA and NTA, have been used as analogues of natural organic ligands in the determination of the chemical forms (Zamuda and Sunda 1982) to quantify the toxicity of dissolved copper as a function of free cupric ion concentration. Copper speciation can be highly variable depending on environmental parameters such as dissolved organic matter, pH, and salinity (Engle et al. 1981). In highly productive coastal waters copper was found to be less toxic because of its ability to form complex molecules and lower cupric ion activities (Sunda and Ferguson 1983).

To make an approximate estimate of ionic copper in the tests performed, data for particulate, organic and inorganic fractions of copper in seawater in the vicinity of our laboratory were obtained from Montgomery and Santiago (1978). By deducting the above fractions from the total concentration, we estimated the ionic copper as 1% of the total measured. This calculated fraction of 1% falls within the reported range for the free ion, Cu^{++}, in natural marine systems. Zirino and Yamamoto (1972) indicated that the fraction of total copper which was ionic (at 25°C and 19 ppt) ranged from 0.1% above pH 8.6 to 30% at pH 7. Both the pH (7.8 to 8.1) and the salinity (35.5 to 36.5 ppt) of the test system would favor the establishment of low ionic copper concentrations in the experimental system used.

Sublethal effects of copper were demonstrated in three of the four conch responses studied. Reduction in grazing and fecal pellet production and inhibition of righting response are all sublethal effects that could significantly affect long-term survival of conch juveniles. Considering that the effective copper is 1% of the total, such sublethal effects may result from concentrations as low as 0.3 $\mu g \cdot \ell^{-1}$.

Under the experimental conditions, no sublethal effect of copper on growth was observed. Although conch growth

TABLE 1.

Observed mortality of conchs exposed to two concentrations of copper during 96-hour bioassays.

Initial Total Copper Concentation $\mu g \cdot \ell^{-1}$	% Mortality (N = 15 per test)			
	24h	48h	72h	96h
0 (control)	0	0	0	0
400	0	0	0	20
1,100	0	13	100	100

during the static bioassay was significant [similar to that of laboratory-reared conchs which were held in captivity during October 1982 (0.15 mm · day^{-1}; Appeldoorn and Ballantine 1983)], minimum conch growth occurred between late February and early April for similar size conchs in both the laboratory and field (Appeldoorn, pers. comm.). Considering the significant reduction observed in grazing rates in exposed individuals, it seems possible that if copper exposures had been longer or conducted during months when higher growth rates have been observed (Alcolado 1976), an effect of treatment on growth would have been noticed. Although overlapping in range, the mean growth for control conchs was higher than for exposed conchs. Copper is known to inhibit growth in other molluscan species. For example, the Atlantic bay scallop *Argopecten irradians* Lamarck, a temperate marine bivalve, showed a growth reduction when exposed to a total copper concentration which was one order of magnitude lower than that used in this experiment (Pesch et al. 1979).

Grazing and fecal production rates of conchs were reduced by copper concentrations as low as 30 $\mu g \cdot \ell^{-1}$ total (presumed ionic concentration = 0.3 $\mu g \cdot \ell^{-1}$). Fluctuations in daily rates could be attributed to such factors as: condition of the algae, hunger level of the conchs, and temperature and pH changes. The positive correlation between fecal pellet production and grazing rates confirms that these two parameters are products of the same process. Similar sublethal effects of copper have been observed in other marine organisms. Fecal pellet and egg production of copepods, feeding activity of the copepod *Acartia clausii* Giesbrecht, and oxygen consumption of *Crassostrea virginica* (Gmelin) were all affected by exposure to total copper in the range of 100 $\mu g \cdot \ell^{-1}$ (Reeve et al. 1977, Engel and Fowler 1979, Moraitou-Apostolopoulou and Verriopoulos 1979).

One of the important behavioral activities of conchs is the righting response by which they can escape predation and regain normal orientation after disturbance (Berg 1975). Observations made of the southern stingray *Dasyatis americana* Hildebrand and Schroeder as it fed on conchs indicate that by disturbing the substrate it overturns the conchs and then grabs the exposed foot (Randall 1964). Loss of the ability to return to the normal foot-down position when overturned increases the susceptibility of conchs to predation. The time required to right varies among individuals. *Strombus gigas* turned over more rapidly than did *S. gallus* Linné (Berg 1975). This righting behavior is a useful indicator in toxicity tests that seek to identify easily observed responses that give a clear indication of an effect of a pollutant.

Although the LC_{50} for juveniles of *Strombus gigas* could not be determined from the toxicity test, the results show that it lies between 400 and 1,000 $\mu g \cdot \ell^{-1}$ and probably closer to 400 $\mu g \cdot \ell^{-1}$ of total copper (presumed ionic copper equivalent of 4 $\mu g \cdot \ell^{-1}$). This estimated LC_{50} is higher than that reported for other tropical molluscs such as *Donax denticulatus* Linné and *Crassostrea madrasensis* Preston (Kumaraguru and Ramamoorthi 1978, Zimmerman et al. 1981), but at least part of these differences could be related to total versus ionic partitioning effects. No other data for copper toxicity in tropical marine gastropods could be found. Analyses of the urchin *Lytechinus variegatus* (Lamarck), which was collected while feeding in metal-rich environments along the western coast of Puerto Rico, revealed a net uptake of copper (Montgomery and Price 1979). Thus, there exists the possibility that populations of *Strombus gigas* which live in the same area may continuously experience a low level of copper stress. This is cause for concern and, considering both the ecological and commercial importance of conchs and the results of this study, a further examination of the effects of copper on egg development and larval growth of *Strombus gigas* would be prudent.

ACKNOWLEDGMENTS

I express my gratitude to many members of the Marine Ecology Division of the Center for Energy and Environment Research who in various ways, assisted in this study. I greatly appreciate the help of Dr. Laurence J. Tilly and Gary P. Owen with the experimental design and manuscript review. Dennis Corales helped in the laboratory and algal field collections; Dr. Alan P. Covich carefully reviewed the manuscript and provided editorial remarks, and Dr. Jose M. Lopez advised on the chemical analysis. Ms. Terry Robles typed and edited the manuscript. I also especially thank Dr. Richard S. Appeldoorn of the Marine Sciences Department of the University of Puerto Rico for comments on the manuscript and encouragement to publish this work. The juvenile conchs were kindly provided by Drs. D. Ballantine and R. Appeldoorn.

REFERENCES CITED

Ahsanullah, M., D. S. Negilski & M. C. Mobley. 1981. Toxicity of zinc, cadmium and copper to the shrimp *Callianassa australiensis*. I. Effects of individual metals. *Mar. Bio. (Berl.)* 64:299–304.

Alcolado, P. M. 1976. Growth, morphological variations of the shell and some biological data of the conch ("cobo") *Strombus gigas* (Mollusca, Mesogastropoda). *Acad. Cienc. Cuba Scr. Oceanolo.* 34:36 p.

Appeldoorn, R. S. & D. L. Ballantine. 1983. Field release of cultured queen conchs in Puerto Rico: implications for stock restoration. *Proc. Gulf Caribb. Fish. Inst.* 35:89–98.

_____ & P. Chantey. 1983. Observations on the growth and survival of laboratory-reared juvenile conchs, *Strombus gigas* Linné and *S. coastatus* Gemlin. *J. Shellfish Res.* 3(1):82 (Abstract).

ASTM. 1980. *Standard Practice for Conducting Acute Toxicity*

Tests with Fishes, Macroinvertebrates and Amphibians. Philadelphia, PA: American Society for Testing and Materials; ASTM Publ. E729–80; 25 p.

Berg, C. J., Jr. 1975. Behavior and ecology of conch (Superfamily Strombacea) on a deep subtidal algal plain. *Bull. Mar. Sci.* 25:307–317.

Davenport, J. & A. Manley, 1978. The detection of heightened seawater copper concentrations by the mussel, *Mytilus edulis. J. Mar. Biol. Assoc. U.K.* 58:843–850.

D'Silva, C. & T. W. Kureishy. 1978. Experimental studies on the accumulation of copper and zinc in the green mussel. *Mar. Pollut. Bull.* 9:187–190.

Engel, D. W. & B. A. Fowler. 1979. Copper and cadmium-induced changes in the metabolism and structure of molluscan gill tissue. Vernberg, W. B.; Thurberg, F. P., Calabrese, A.; Vernberg, F. J. eds. *Marine Pollution: Functional Responses.* New York, NY: Academic Press; 239–255.

Engel, D. W. & W. G. Sunda. 1979. Toxicity of cupric ion to eggs of the spot *Leiostomus xanthurus* and the Atlantic silverside *Menidia menidia. Mar. Biol. (Berl.)* 50:121–126.

_____ & B. A. Fowler. 1981. Factors affecting trace metal uptake and toxicity to estuarine organisms. I. Environmental parameters. Vernberg, F. J.; Calabrese, A.; Thurberg, F. P.; Vernberg, W. B. eds. *Biological Monitoring of Marine Pollutants.* New York, NY: Academic Press; 127–144.

Kumaraguru, A. K. & K. Ramamoorthi. 1978. Toxicity of copper to three estuarine bivalves: *Anadara granosa, Meretrix casta* and *Crassostrea madrasensis. Mar. Environ. Res.* 1(1):43–48.

Kumaraguru, A. K., D. Selvi & V. K. Venugopalan. 1980. Copper toxicity to an estuarine clam, (*Meretrix casta*). *Bull. Environ. Contam. Toxicol.* 24(6):853–857.

Lowman, F. G., D. K. Phelps, R. McClin, V. Roman de Vega, I. Oliver de Padovani & R. J. Garcia. 1966. Interactions of the environmental and biological factors on the distribution of trace elements in the marine environment. *Disposal of Radioactive Wastes into Seas, Oceans and Surface Waters.* Vienna, Switzerland: International Atomic Energy Agency; 249–266.

Montgomery, J. R. & R. J. Santiago. 1978. Zinc and copper in "particulate" forms and "soluble" complexes with inorganic or organic ligands in the Guanajibo River and coastal zone, Puerto Rico. *Estuarine Coastal Mar. Sci.* 6:111–116.

Montgomery, J. R. & M. T. Price. 1979. Release of trace metals by sewage sludge and the subsequent uptake by members of a turtle grass mangrove ecosystem. *Environ. Sci. Technol.* 13:546–549.

Moraitou-Apostolopoulou, M. & G. Verriopoulos. 1979. Some effects of sublethal concentrations of copper on a marine copepod. *Mar. Pollut. Bull.* 10:88–92.

Nriagu, J. O., ed. 1979. *Copper in the Environment. Part 2: Health Effects.* New York, NY: Wiley-Interscience; 489 p.

Pesch, G., N. Steward & C. Pesch. 1979. Copper toxicity to the Bay Scallop (*Argopecten irradians*). *Bull. Environ. Contam. Toxicol.* 23:759–765.

Randall, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas. Bull. Mar. Sci. Gulf Caribb.* 14:246–295.

Reeve, M. R., M. A. Walter, K. Darcy & T. Ikeda. 1977. Evaluation of potential indicators of sub-lethal toxic stress on marine zooplankton (feeding, fecunity, respiration and excretion): controlled ecosystem pollution experiment. *Bull. Mar. Sci.* 27:105–113.

Sokal, R. R. & F. J. Rohlf. 1981. *Biometry.* San Francisco, CA: W. H. Freeman and Co.; 859 p.

Sprague, J. B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. *Water Res.* 3:793–821.

_____ . 1976. Current status of sublethal tests of pollutants on aquatic organisms. *J. Fish. Res. Board Can.* 33:1988–1992.

Steele, C. W. 1983. Acute toxicity of copper to sea catfish. *Mar. Pollut. Bull.* 14(5):168–170.

Sullivan, B. K., E. Buskey, D. C. Miller & P. J. Ritacco. 1983. Effects of copper and cadmium on growth, swimming and predator avoidance in *Eurytemora affinis* (Copepoda). *Mar. Biol. (Berl.)* 77:299–306.

Sunda, W. & R. R. L. Guillard. 1976. The relationships between cupric ion activity and the toxicity of copper to phytoplankton. *J. Mar. Res.* 34:511–529.

Sunda, W. G. & R. L. Ferguson. 1983. Sensitivity of natural bacterial communities to additions of copper and to cupric ion activity: a bioassay of copper complexation in seawater. Wong, C. S.; Boyle, E; Bruland, K. W.; Burton, J. D. eds. *Trace Metals in Sea Water.* New York, NY:Plenum Publishing Corp.; 871–891.

Timourian, H. & G. Watchmaker. 1972. Nickel uptake by sea urchin embryos and their subsequent development. *J. Exp. Zool.* 182:379–388.

Zamuda, C. D. & W. G. Sunda. 1982. Bioavailability of dissolved copper to the American oyster *Crassostrea virginica.* I. Importance of chemical speciation. *Mar. Biol. (Berl.)* 66:77–82.

Zimmerman, R., E. Hawk & I. Sanders. 1981. Comparative acute toxicities of copper, zinc and nickel to marine organisms and data on tolerances from Puerto Rico. (Unpublished manuscript) Available from: University of Puerto Rico, Mayaguez, Puerto Rico.

Zirino, A. & S. Yamamoto. 1972. A pH-dependent model for the chemical speciation of copper, zinc, cadmium and lead in seawater. *Limnol. Oceanogr.* 17(5):661–671.

Journal of Shellfish Research, Vol. 4, No. 1, 37–43, 1984.

THE EFFECT OF SIZE ON MORTALITY OF SMALL JUVENILE CONCHS (*STROMBUS GIGAS* LINNÉ AND *S. COSTATUS* GMELIN)

RICHARD S. APPELDOORN
Department of Marine Sciences
University of Puerto Rico
Mayagüez, Puerto Rico 00708

ABSTRACT The effect of size on the mortality rate of small juvenile conchs was investigated using short-term mark-recapture experiments. Two size groups each of laboratory-reared *Strombus gigas* Linné and *S. costatus* Gmelin were released offshore on a sand and macroalgal plain. Mortality was estimated using the Jolly-Seber method and by using the proportion of dead conchs to total conchs observed during each survey. The two methods generally yielded consistent results. Rates of mortality varied during experiments by a factor of 6. For both species, larger conchs suffered less mortality. Among narrowly defined size classes, the ratio of mortality rates varied only slightly, regardless of changes in the overall magnitude of mortality. Among dead conchs recovered, significant differences were observed in patterns of shell breakage between large and small conchs and between species. These differences may be explained by differences in shell size and morphology.

KEY WORDS: *Strombus*, survival, mortality, predation

INTRODUCTION

The life history of marine planktotrophic organisms is typically characterized by very high mortality during early-life stages (Thorson 1966). Slobodkin (1962) presented four generalized survivorship curves of which two, Types III and IV, describe the above pattern. Species displaying the Type III curve have a constant rate of mortality (percent mortality/time) and survivorship is described as a decreasing exponential function. With curve IV, rate of mortality decreases over time. Slobodkin stated that curve IV was probably most common, but that rate of mortality stabilized with age and curve III was then adequate to model species survivorship. Studies have verified this for a wide variety of species and, in general, the period of decreasing mortality rate is short relative to the life span of the species. Indeed, a constant rate of mortality over the life span considered (e.g., after recruitment) is a major assumption of most fisheries models, e.g., yield per recruit (Beverton and Holt 1957) and virtual population analysis (Gulland 1965). Such an assumption, however, cannot be made when dealing with early-life history or in studies of species whose rate of mortality does not quickly stabilize.

Previously, Appeldoorn and Ballantine (1983) presented evidence suggesting that mortality rates of the queen conch *Strombus gigas* Linné decreased significantly over a relatively long period of time. Queen conchs enter the fishery as much as one year prior to sexual maturity (personal observation), but constant mortality may not be achieved until the onset of maturity when shell growth in length ceases and the flared lip of the shell is formed. This preliminary analysis was based primarily on the results of Randall (1964) and Alcolado (1976), both of whom studied large juveniles. To date, little work has been done relating the change in mortality with size/age in small (< 50 mm) conchs. The purpose of this paper is to report on two mark-recapture experiments in which mortality was compared among different size classes of small conchs. Two species, *S. gigas* and the closely related milk conch *S. costatus* Gmelin, were studied.

MATERIALS AND METHODS

Methods employed were similar to those previously reported in detail by Appeldoorn and Ballantine (1983). Those methods are briefly outlined here. All animals were laboratory reared from field-collected eggs (Ballantine and Appeldoorn 1983). Conchs were tagged prior to release by gluing a 75-mm thin, flexible strip of brightly colored polyethylene to the tip of the spire. Using a fine-tip, permanent-marking pen each tag was individually numbered at both its base and tip to ensure identification regardless of tag breakage. All further analyses deal only with the population of tagged and released conchs.

The study area was located on a calcareous sand and macroalgal plain located 5 km south of La Parguera, Puerto Rico, at a depth of 17 m. The area consisted of a 16-m radius circle centered around the point of release. At release all conchs were individually placed under the sediment surface to reduce exposure. The study area was surveyed by divers every two weeks for eight weeks. During each survey all tagged conchs found alive were enumerated and tag numbers recorded. Any conchs found in the outer 4 to 5 m were repositioned near the center to reduce emigration. Dead individuals were collected and sorted according to shell type. Classifications of dead returns were crushed shells (with only a portion of the shell attached to the tag), spirally cut shells (with the body whorl progressively cut back around the axis of the shell), and whole shells (with the shell empty but undamaged).

Mortality was estimated using two methods. The first estimate was calculated as the proportion or ratio of dead

conchs to total conchs observed, hereafter referred to as the ratio method (Appeldoorn and Ballantine 1983). Estimates were made for each of the four sampling periods. The second estimate was made using the Jolly-Seber method of tag return analysis (Seber 1982). This method is appropriate for open populations where emigration, death, etc., occur during the experiment. Its use here is slightly modified because the original population size (number of released conchs) is known and the entire population is tagged at the time of release. The equations given by Seber (1982; p. 200) permit an estimation of survival (s) during each of the first three sampling periods, and population size at the time of samples 1, 2, and 3. The estimates were unadjusted for bias because, with high-sampling efficiency and low coefficients of variation, little bias would be expected and adjustment is then unnecessary (see Seber 1982; Section 13.1.2 for additional discussion on bias and the properties of adjusted and unadjusted estimates). Variances for these estimates can also be calculated (Seber 1982; p. 202). Mortality was calculated as $a = 1 - s$. Jolly-Seber estimates include losses due to both death and permanent emigration. For each mortality estimate, the instantaneous rate of mortality, $z = -\ln(a)$, was calculated, with time expressed in years (Ricker 1975). Within each period, the decline of the tagged population can then be described by:

$$N_t = N_O \exp -zt$$

where N_O is the population size at the start of the period, and N_t is the number surviving after time t; e.g., for a 14-day sampling period, $t = 0.038$ year.

The first experiment began in mid-January 1983 and involved the release of two size groups of each species. Each group of *S. gigas* contained 112 individuals. The small size group ranged from 22 to 35 mm ($\bar{x}$ = 29.6 mm); the large group ranged from 35 to 57 mm ($\bar{x}$ = 39.8 mm) in length. For *S. costatus* the small group was similar to that of *S. gigas*, containing 115 individuals ranging from 22 to 37 mm ($\bar{x}$ = 29.9 mm) in length; however, only a small number of large *S. costatus* were available and, to increase the chances of observing size-dependent mortality differences, the size range employed was much greater than for *S. gigas*. Forty individuals were used ranging from 42 to 89 mm ($\bar{x}$ = 55.3 mm) in length.

A second experimental release of two size groups of *S. costatus* was made in mid-March. At that time 60 large conchs were released, ranging from 32 to 72 mm ($\bar{x}$ = 43.2 mm) in length. The small group contained 106 conchs which ranged from 20 to 32 mm ($\bar{x}$ = 25.2 mm) in length.

RESULTS

Table 1 presents the recapture data for both experiments. These data were used to calculate the parameters for the Jolly-Seber estimates. At each sampling, recovery rates of live and dead conchs were generally from 70% to 80% for all groups except the large individuals of *S. costatus*. Here the rate was approximately 50% to 60%. Mortality estimates for the first experiment are shown in Table 2. The agreement between mortality estimates made by the two methods was unexpectedly close considering the confidence of the estimates. As expected, standard errors obtained for the Jolly-Seber method increased with time as population size, and hence sample size, decreased.

For both size groups of *S. gigas*, the instantaneous rate of mortality (z) increased during the course of the experiment, varying approximately by a factor of 6. The effect of size on mortality can be seen by taking the ratio of large conch mortality to small conch mortality. This ratio varied somewhat between sampling periods, but the variations were independent of the absolute magnitude of mortality. Indeed, by the ratio method of mortality estimation, z for the large group remained relatively constant, at approximately 40% that of the small group. Ratios of instantaneous rates of mortality between size classes obtained by the Jolly-Seber method were more variable. For the second sampling period this ratio was approximately one, but the large disparity between the magnitude of mortality estimated by each method within the large size group may indicate an overestimation by the Jolly-Seber method. For small individuals of *S. costatus* the pattern of mortality was similar to that of *S. gigas*. For large individuals of *S. costatus*, however, mortality was considerably lower, especially toward the end of the experiment.

To put the results in a different perspective, mortality estimates can be used to calculate the proportion of conchs that survived throughout the experiment. Regardless of the method used, after 6 weeks the proportion of small individuals of *S. gigas* surviving was only one half that of large individuals of *S. gigas*. After 8 weeks this proportion dropped to 28%. For *S. costatus* the respective survival of small-to-large conchs was roughly 45% and 22%.

Results of the second experiment are shown in Table 3. Initially, no overall patterns of mortality were apparent between size groups. Inspection of the recapture data indicated that the largest milk conchs were not being sampled (see **Discussion**), thus violating the assumption of equal probability of recapture. This results in higher estimates of mortality and lower estimates of population size. The largest 15 conchs, ranging from 45 to 72 mm in length, were, therefore, excluded from the data and the analysis repeated. Recalculation showed that mortality in the large group was less than in the small group for the first two sampling periods and approximately equal for the third. The proportion of small conchs surviving the experiment was less than that for large conchs, but the relative difference between the two was not as great as observed in the prior experiment.

TABLE 1.

Tabulation of the number of conchs caught in the *i*th sample last captured in the *h*th sample (after Seber 1982).*

Experiment Begun 25 January 1983

Strombus gigas – Large

	i	0	1	2	3	4	
	n_i	112	93	79	46	21	
h	R_i	112	93	79	46		r_h
0			93	6	0	0	98
1				73	1	1	75
2					45	5	50
3						15	15
	m_i	0	93	79	46	21	

Strombus gigas – Small

	i	0	1	2	3	4	
	n_i	112	76	69	28	7	
h	R_i	112	76	69	28		r_h
0			76	12	1	0	89
1				57	2	0	59
2					25	1	26
3						6	6
	m_i	0	76	69	28	7	

Strombus costatus – Large

	i	0	1	2	3	4	
	n_i	40	23	20	13	12	
h	R_i	40	23	20	13		r_h
0			23	8	0	0	31
1				12	3	2	17
2					10	4	14
3						6	6
	m_i	0	23	20	13	12	

Strombus costatus – Small

	i	0	1	2	3	4	
	n_i	115	87	66	27	9	
h	R_i	115	87	66	27	9	r_h
0			87	5	0	0	92
1				61	2	1	64
2					25	1	26
3						7	7
	m_i	0	87	66	27	9	

Experiment Begun 25 March 1983

Strombus costatus – Large

	i	0	1	2	3	4	
	n_i	60	26	25	12	6	
h	R_i	60	26	25	12		r_h
0			26	7	3	0	36
1				18	0	0	18
2					9	2	11
3						4	4
	m_i	0	26	18	12	6	

Strombus costatus – Small

	i	0	1	2	3	4	
	n_i	106	57	40	23	10	
h	R_i	106	57	40	23		r_h
0			57	9	1	0	67
1				31	1	0	32
2					21	2	23
3						8	8
	m_i	0	57	40	23	10	

*LEGEND:

n_i = number of conchs caught in the *i*th sample

R_i = number of conchs released at the *i*th sample

r_h = total number of conchs recaptured, last caught in the *h*th sample

m_i = number of conchs recaptured in the *i*th sample

0th sample represents the time of release

TABLE 2.

Proportion of mortality and instantaneous mortality rate (z) for large and small size groups of *Strombus gigas* and *S. costatus* during each sampling period for the experiment beginning 25 January 1983.*

Size Group	Period	Duration (Days)	Number of Dead Conchs Recovered	Method	Proportion of Mortality	Z
			Strombus gigas			
Small	1	17	17	R	0.183	4.33
				JS	0.172 (0.042)	4.05
	2	11	11	R	0.143	5.11
				JS	0.170 (0.061)	6.18
	3	14	29	R	0.509	18.53
				JS	0.574 (0.084)	22.31
	4	14	14	R	0.667	28.64
Large	1	17	9	R	0.088	1.98
				JS	0.103 (0.032)	2.34
	2	11	5	R	0.062	2.12
				JS	0.182 (0.042)	6.67
	3	14	15	R	0.250	7.50
				JS	0.216 (0.100)	6.35
	4	14	12	R	0.369	11.78
			Strombus costatus			
Small	1	17	18	R	0.171	3.71
				JS	0.162 (0.038)	3.79
	2	11	14	R	0.221	8.28
				JS	0.215 (0.059)	8.03
	3	14	32	R	0.542	20.38
				JS	0.529 (0.096)	19.63
	4	14	9	R	0.500	18.07
Large	1	17	3	R	0.115	2.49
				JS	0.155 (0.082)	3.62
	2	11	2	R	0.091	3.17
				JS	0.198 (0.107)	7.31
	3	14	1	R	0.071	1.93
				JS	0.042 (0.219)	1.12
	4	14	1	R	0.077	2.09

*LEGEND:

z is expressed with time in years, i.e., the rate expected if the observed rate for each sampling period remained constant over one year.
JS indicates results using the Jolly-Seber method
R indicates results using the ratio of dead to total conchs
Values in parentheses are standard deviations (SD) derived from the Jolly-Seber estimates of survival.

In the first experiment significant differences were observed between species and between size groups in the proportions of dead shell types recovered (Table 4). For *S. gigas* more whole shells were found from the large group than from the small group ($\chi^2 = 7.58$, df = 1, p = 0.006). More spiral shells were also found from the large group but the difference was not statistically significant. Comparing small individuals of *S. gigas* and *S. costatus*, I found that the latter yielded significantly more spiral shells ($\chi^2 = 5.30$, df = 1, p = 0.022). No comparisons were made with dead shell returns of large individuals of *S. costatus* in the first experiment because of low sample size. In the second experiment a higher proportion of whole shells was found from the large group (22% versus 9%) but the difference was not statistically significant ($\chi^2 = 2.12$, df = 1, p = 0.15).

DISCUSSION

In most tagging experiments recaptures account for only a small percentage of the total marked population. For precision, it is, therefore, necessary to tag a large fraction of the population. Studies based on small sample sizes additionally require a high sampling efficiency. In the present study the recapture rate was very high, and 100% of the population was marked; these are prerequisites if the estimates obtained are to be considered reliable. Coefficients

TABLE 3.

Proportion of mortality and instantaneous mortality rate (z) for large and small size groups of *Strombus costatus* during each sampling period for the experiment beginning 25 March 1983.†

Size Group	Period	Duration (Days)	Number of Dead Conchs Recovered	Method	Proportion of Mortality	Z	Z^*
Small	1	13	24	R	0.296	9.87	
				JS	0.292 (0.060)	9.77	
	2	15	25	R	0.387	11.81	
				JS	0.419 (0.066)	13.21	
	3	14	13	R	0.361	11.68	
				JS	0.396 (0.009)	13.14	
	4	14	9	R	0.472	16.73	
Large	1	13	11	R	0.297	9.91	8.07
				JS	0.326 (0.080)	11.08	7.34
	2	15	4	R	0.138	3.61	3.90
				JS	0.213 (0.121)	5.83	4.12
	3	14	9	R	0.429	14.59	13.32
				JS	0.434 (0.170)	14.84	12.67
	4	14	7	R	0.538	20.16	20.16

†LEGEND:
z is expressed with time in years, i.e., the rate expected if the observed rate for each sampling period remained constant over one year.
JS indicates results using the Jolly-Seber method.
R indicates results using the ratio of dead to total conchs.
Z^* is the calculated instantaneous mortality rate after excluding the largest 15 conchs from the analysis.
Values in parentheses are standard deviations (SD) derived from the Jolly-Seber estimates of survival.

TABLE 4.

Percentage of dead shell types recovered for large and small size groups of *Strombus gigas* and *S. costatus* during the experiment beginning 25 January 1983. (Total numbers of dead shells recovered are given in parentheses.)

	Strombus gigas		*Strombus costatus*	
Shell Type	Small (67)	Large (39)	Small (72)	Large (4)
Whole	8.9	32.1	8.3	25.0
Crushed	85.1	53.8	70.8	75.0
Spiral	6.0	14.1	20.8	0.0

of variation for the estimates of survival obtained by the Jolly-Seber method were generally under 10% for the first two periods and 10% to 20% for the third.

Jolly-Seber estimates should overestimate mortality because emigration is included in the estimate. In practice, however, no evidence for this was apparent. Juvenile milk conchs are not highly vagile (Appeldoorn and Ballantine 1983, Appeldoorn, in press) and emigration should have been of little importance within the time frame of the experiments; however, queen conch emigration could have been significant despite replanting efforts. Nevertheless, Jolly-Seber estimates showed no greater degree of mortality than did ratio estimates. Relative to the reliability of the estimates, then, emigration did not appear to have been significant.

Estimates obtained by the ratio method were based on the assumption that tags on dead and live snails were equally visible. This was thought, generally, to be the case with the possible exception of the largest milk conchs. Their lower probability of capture may have been caused by deeper burial, which submerged the tag beneath the sediment. Typically, dead shells were found on the surface and an artificially high proportion of dead shells may have been calculated.

The magnitude of mortality may have been affected by other factors such as tag loss, attraction of predators to tags, or predator response to variations in conch density. In previous studies (Appeldoorn and Ballantine 1983), all tag losses resulted from tag breakage. Such tags were still visible, but lacked the identification number. In the present experiments this problem was overcome by numbering tags at both ends. Predator attraction to tags was probably insignificant. Laboratory observations indicated no effect on predation by spiny lobsters, an important crustacean predator (Appeldoorn and Ballantine 1983). Potential predatory fish seemed to be attracted only by the kicking motion of the conch's foot, not by the tag (personal observation), and no successful attacks were observed. The burying of conchs at release was designed to reduce the risk of such predation. The effects of conch density on mortality are unknown. Small juveniles in the natural population are rarely seen, so their density has not been estimated. Experimental conchs were most dense at release. In the present experiments predation was lowest at this

time, but, in general, there seemed to be no relationship between mortality and experimental conch density (Appeldoorn, in press). Therefore, from the available evidence, there is no reason to suspect a systematic bias in the mortality rates observed. If such a bias did occur, however, it should have affected both large and small conchs equally and, therefore, have had little impact on results because the concern here was more on the relative differences in mortality between size groups rather than on the actual magnitude of mortality.

In general, estimates obtained by both methods appear to be valid. The close agreement between methods supports this claim and indicates that the confidence of the estimates is perhaps greater than that indicated by the Jolly-Seber variance estimates alone. The comparison of large and small queen conchs in the first experiment is considered to be the most reliable because both groups had an equal and large number of individuals, and because the size distribution in each group was controlled within a narrow range. This allowed for more precision in the quantitative evaluation of the effect of size on mortality.

An average of mortality ratios between large and small individuals of *S. gigas* at all periods indicated that mortality decreased by approximately 50% over an average size of 10 mm. During warmer months, 10 mm of growth required about two months (Appeldoorn and Ballantine 1983, Appeldoorn, in press). Data of Randall (1964) showed that mortality rate decreased by approximately 50% between 1.1 and 2.3 years of age. Jory and Iversen (1983) reported that the number of predator species and, by inference, predation dropped significantly after conchs reach 100 to 150 mm in length. It appears that mortality rate decreases significantly with increasing size over an extended range, but that the decrease was disproportionately greater at small sizes. Saila and Lough (1981) used a Weibull hazard function to describe a similar decline in instantaneous mortality rate (z) over the larval life of herring. Such a function would seem appropriate to model the dynamics of conch mortality rates when more precise first-year mortality estimates become available. It could then be employed to predict survivorship in fisheries models or mariculture programs.

The extended decline of the mortality rate of *S. gigas* with age indicates a significant Type-IV survivorship pattern (Slobodkin 1962). This differs from observations made on most other species. The pattern of mortality described here is probably most appropriately compared to that reported by Miyamoto et al. (1982) for another gastropod, the abalone *Haliotis discus hannai* Ino. Their release experiments showed that mortality in small abalones decreased rapidly. After 154 days, survival remained nearly constant through the following year and indicated that once a size of 35 to 40 mm was reached the risk of mortality was low. Size-related differences in mortality were only evident at very small sizes. At 154 days, survival of abalones that were less than 22 mm at release was under 10%, while the survival of larger juveniles ranged from 20% to 30%.

Jory and Iversen (1983) surveyed conch predators and their modes of attack. Still, exact causes for patterns of dead shells found in the present study are unknown. The significant differences in the proportions of dead shell types between the various groups is felt to reflect responses by predators to differences in shell size or morphology. Proportionally fewer shells of large individuals of *S. gigas* were crushed than small shells. Larger shells, simply because of increased size and shell thickness, are more difficult to handle and harder to crush. Predators relying on crushing would be hindered or forced to use alternate methods. As an example of the latter, the spiny lobster *Panulirus argus* (Latreille) has been observed crushing small conchs, but peeling larger conchs thereby producing a spiral-shell breakage pattern (personal observation).

A comparison of small individuals of both *S. gigas* and *S. costatus* showed no difference in the proportion of whole empty shells. Differences were found, however, between crushed and spiral-cut shells. *Strombus gigas* was crushed more frequently. Because of their equal length, both species should have been subject to the same array of predators. This would indicate that milk conchs are more resistant to crushing. A comparison of shell morphology between species within the 26- to 35-mm size range showed no significant difference in their length:width relationships, if spine length was included for *S. gigas*. Hence, the ability of predators to manipulate shells should have been equal for both species. Significant differences were found, however, between the length:shell-weight relationships and the length:spire-height relationships. *Strombus gigas* has a higher spire, making it more susceptible to crushing (Vermeij 1978; personal observation), and less shell weight. The latter would indicate either a thinner shell or fewer whorls per length, either of which could reduce the resistence of the shell to crushing (Vermeij 1978). For individuals of *S. gigas* and *S. costatus* of comparable length, some predators may have been forced to spirally cut the shell of the latter, rather than crush it. Alternatively, a weaker queen conch shell may break while being spirally cut. Such breakage is known to occur and the remaining spire, when recovered, would be classified as crushed. There is no evidence from this study to indicate that these differences resulted in any survival differential between the two species.

ACKNOWLEDGMENTS

Thanks are due to A. T. Bardalas, I. M. Sanders and, particularly, D. L. Balantine who helped in all phases of the experiments, and to P. E. Chanley for his major contributions in larval culture. This research was supported, in part, by grants from the National Marine Fisheries Service.

REFERENCES CITED

Alcolado, P. J. 1976. Growth, morphological variations of the shell and some biological data of the conch *Strombus gigas* L. (Mollusca, Mesogastropoda). *Acad. Cienc. Cuba Ser. Oceanol.* 34:26 p. (English translation)

Appeldoorn, R. S. (in press) Growth, mortality, and dispersion of juvenile, laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. *Bull. Mar. Sci.*

_____ & D. L. Ballantine. 1983. Field release of cultured queen conchs in Puerto Rico: implications for stock restoration. *Proc. Gulf Caribb. Fish. Inst.* 35:89–98.

Ballantine, D. L. & R. S. Appeldoorn. 1983. Queen conch culture and future prospects in Puerto Rico. *Proc. Gulf Caribb. Fish. Inst.* 35:57–63.

Beverton, R. J. H. & S. J. Holt. 1957. On the dynamics of exploited fish populations. *G. B. Minist. Agric. Fish. Food Fish. Invest.* Ser. II, 19:533 p.

Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group. *Int. Counc. Explor. Sea. Coop. Res. Rep.* 1965(3):9 p.

Jory, D. E. & E. S. Iversen. 1983. Queen conch predators: not a roadblock to mariculture. *Proc. Gulf Caribb. Fish. Inst.* 35:108–111.

Miyamoto, T., K. Saito, S. Motoya, N. Nishikawa, H. Monma & K. Kawamura. 1982. Experimental studies on the release of the cultured seeds of abalone, *Haliotis discus hannai* Ino in Oshoro Bay, Hokkaido. *Sci. Rep. Hokkaido Fish. Exp. Stn.* 24:59–90.

Randall, J. E. 1964. Contributions to the biology of the queen conch *Strombus gigas*. *Bull. Mar. Sci.* 14:246–295.

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

Saila, S. B. & R. G. Lough. 1981. Mortality and growth estimation from size data – an application to some Atlantic herring larvae. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer.* 178:7–14.

Seber, G. A. F. 1982. *The Estimation of Animal Abundance and Related Parameters.* New York, NY:MacMillan Publishing Co., Inc.; 654 p.

Slobodkin, L. B. 1962. *Growth and Regulation of Animal Populations.* New York, NY: Holt, Rinehart and Winston; 184 p.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* 3:267–293.

Vermeij, G. J. 1978. *Biogeography and Adaptation: Patterns of Marine Life.* Cambridge, MA: Harvard Univ. Press; 332 p.

Journal of Shellfish Research, Vol. 4, No. 1, 45–62, 1984.

BIOLOGY, POPULATION DYNAMICS, AND REPRODUCTION OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ IN THE ARCHIPIÉLAGO DE LOS ROQUES NATIONAL PARK[1]

ERNESTO WEIL M. AND ROGER LAUGHLIN G.
Fundación Científica los Roques
Apartado No. 1, Carmelitas
Caracas 1010A, Venezuela

ABSTRACT Data relating to the distribution, population dynamics, and reproduction of the queen conch *Strombus gigas* Linné at the Archipiélago Los Roques National Park, Venezuela, are presented. Queen conchs were widely distributed in the archipelago and were most abundant in grassbeds [*Thalassia testudinium* (König) and *Syringodium filiforme* Kürtzing] of intermediate depths (4 to 8 m). Juvenile queen conchs were most common in very shallow grassbeds (< 1.0 m deep) that had an abundant food supply and were subjected to low current velocity and little wave action. Queen conch population density and mean shell length were significantly lower in fished than in protected areas. Mean densities of 0.42 ind • m^{-2} were common in unfished areas. Monthly variations in density were minimal in all areas sampled, except for the shallow seagrass beds (< 1.0 m) where massive mortality of queen conchs and the subsequent population recovery structured the monthly abundance curve over a period of 2 years. Results of tag-and-recapture experiments with queen conchs indicated that adults move constantly and over considerable distances (1 to 4 km) when the seagrass beds they inhabited were very large. Juveniles moved very little and remained in small areas over long periods of time (> 1 year). Natural mortality was estimated at 2.08 ind • mo^{-1} for a shallow grassbed (> 1.0 m deep) and was caused primarily by desiccation during periods of extreme low tides, and by fish and invertebrate predation.

The reproductive season extends from late April to late November and appeared to be controlled by water temperature. The reproductive intensity, assessed by the number of egg masses • m^{-2} of substrate, was highest in seagrass beds at depths ranging from 4 to 8 m, and was possibly related to conch population density. The highest density of egg masses was 8 m^{-2} of substrate. In Los Roques, a female conch is capable of laying three to four viable eggs masses per month; this is equivalent to a maximum of 25 egg masses per female in a breeding season which is a value substantially higher than has been reported in the literature. Many females were observed copulating and laying eggs simultaneously. An egg mass of a mean length of 14 cm may contain a mean of 700,000 eggs. The sex ratio was 1:1. Natural growth rate of conchs varied from 0.4 to 1.5 cm in shell length per month, with a mean of 0.9 cm • mo^{-1}, a value considered relatively high. Recruitment appeared to occur primarily in shallow seagrass beds during the summer months. Recruitment of conchs to depopulated areas appeared to be very high and capable of reestablishing natural abundances in very short periods of time.

KEY WORDS: *Strombus gigas*, queen conch, population dynamics distribution, reproduction, growth, migration, Venezuela.

INTRODUCTION

The queen conch *Strombus gigas* Linné is a large marine snail which is widely distributed on sandy bottoms and seagrass (*Thalassia testudinium* [König] and *Syringodium filiforme* Kürtzing) beds throughout the Caribbean Sea (Randall 1964, Brownell and Stevely 1981). *Strombus gigas* is the object of an active fishery. Although the resource still holds commercial importance, it has been exhausted in many regions by overfishing (Brownell and Stevely 1981).

In Venezuela, queen conchs are found almost exclusively in the Archipiélago de Los Roques National Park and the Archipiélago Las Aves. In 1975 a culture project was begun at Los Roques with the idea of restocking overfished areas in the region (Brownell 1977). Brownell's work was followed by a large-scale study on queen conch ecology, mariculture, fishery, and stock recovery. Aspects of the culture technique for *S. gigas* have already been published (Laughlin 1983, Laughlin and Weil 1983). In this paper we present information on the ecology of *S. gigas* with special emphasis given to population dynamics, distribution, reproduction, and migration.

Study Area

The Archipiélago de Los Roques National Park is an insular reef complex located approximately 150 km north of the north-central coast of Venezuela (Figure 1). It forms an irregular oval of 36.6 × 24.6 km on the east-west and the north-south axes, respectively, and consists of 42 islands and more than 200 sandbanks and reefs distributed around a shallow lagoon (depth 1 to 5 m) on its centromeridional portion. The archipelago rests on a submarine igneous plateau that rises sharply from depths of 900 to 1,000 m. The winds and ocean currents are predominantly from the east-northeast. The climate could be classified as arid-humid with a mean annual precipitation of 30.0 cm.

Intensive studies were conducted in the southwestern region of the archipelago, especially in the area surrounding the Dos Mosquises Marine Station of the Fundación Científica

[1] Scientific contribution number 18 of the Fundación Científica Los Roques.

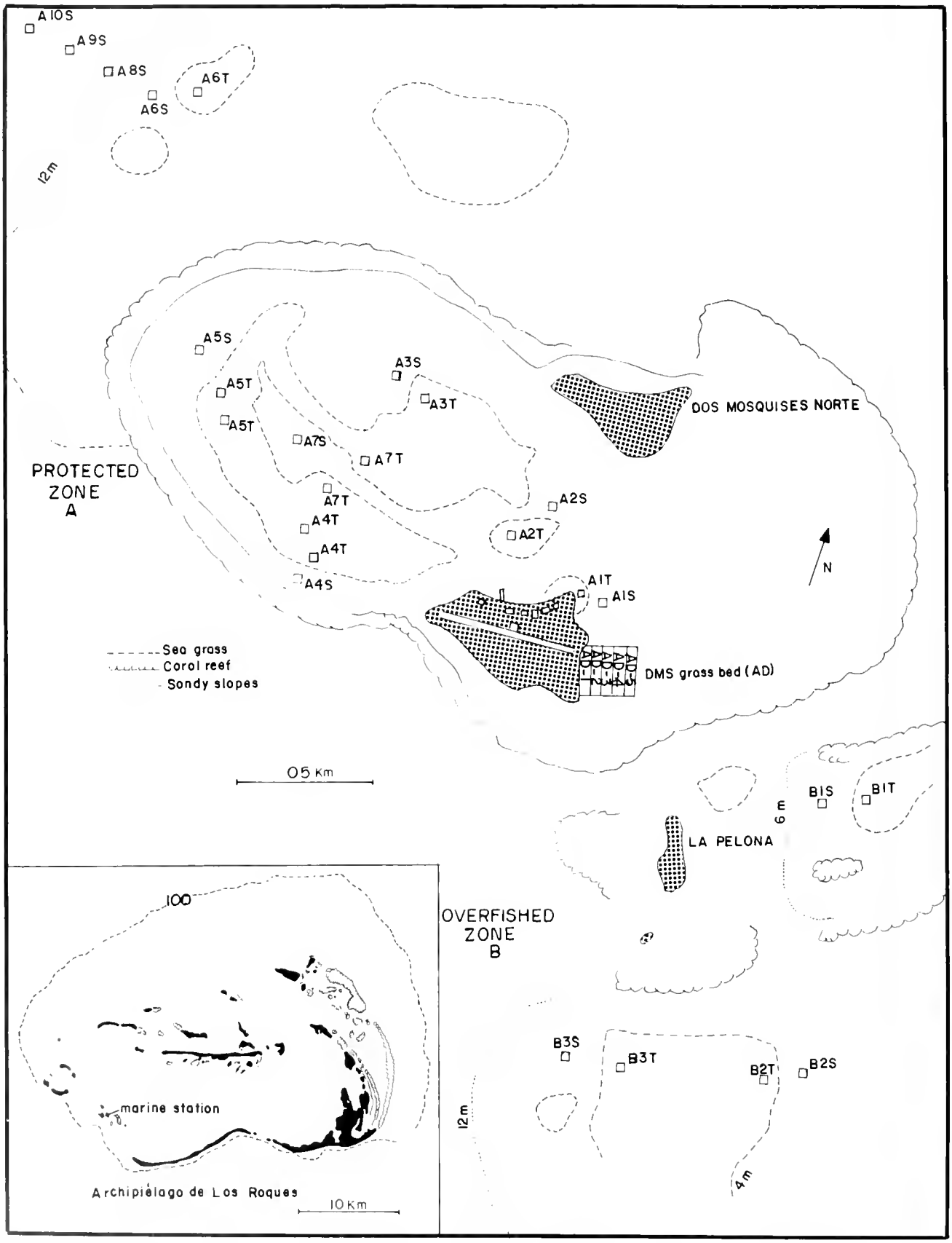


Figure 1. Map of the study area with an indication of sampling stations. The codes S and T refer to open sand and grassbeds (*Thalassia testudinium*), respectively .

Los Roques (Figure 1). The study area was divided into two sampling zones; the "protected zone" (Zone A), where queen conch fishing is prohibited, has an approximate area of 4.0 km^2 and is formed by an internal platform with depths between 0.10 and 8.0 m, and an external platform which extends to the west, with depths increasing gradually, to a sandy slope which drops to 18.0 m. Both platforms are separated by a shallow (1.5- to 2.5-m) horseshoe-shaped reef formed mainly by the coral species *Acropora cervicornis* (Lamarck), *A. palmata* (Lamarck), and *Montastrea annularis* (Ellis and Solander). About 70% of the substrate of the internal platform is covered by the seagrass species *Thalassia testudinum* and *Syringodium filiforme*, and by algae; the rest is covered by calcareous sand with a few patches of *A. cervicornis*, *M. annularis* and *Siderastrea siderea* (Ellis and Solander). The substrate of the external platform is mostly sand with patches of *S. filiforme* and *T. testudinum* (Figure 1). Within the protected zone, to the east of Dos Mosquises-Sur, there is a coastal grassbed of *T. testudinum* which covers approximately 3,000 m^2. It is referred to in this paper as the Dos Mosquises-Sur (DMS) grassbed (AD) (Figure 1) and was the site of this intensive study of queen conch population dynamics. That sea grassbed is subjected to extreme low tides from April to July; during that period almost 80% of the grassbed area is exposed to the air and direct sunlight. Water temperature in this grassbed ranged from 29° to 33°C and in the tidepools it reached 36°C at noon. Salinity varied little (39 to 41 ppt). A barrier reef which reduces wave action and current velocity is located east of the study site.

The unprotected or fished zone (Zone B) corresponds to those nearby areas where an intensive queen conch fishery is taking place and other fished areas such as Cayo Sal, Bequeve, Isla Fernando, etc., where occasional observations were made.

MATERIALS AND METHODS

Queen conch density and mean shell length were estimated in the protected (A) and fished (B) areas using fixed 25-m^2 quadrats made of steel bars and nylon cord. In the protected zone (A), the quadrats were placed along a depth gradient from 1.0 to 18.0 m. The depths selected with their respective coded identifications were: 1.0 m (A1T, A1S); 4.0 m (A2T–A2S, A3T–A3S, A4T–A4S); 6.0 m (A5T–A5S, A6T–A6S); 8.0 m (A7T–A7S); 12.0 m (A8S); 15.0 m (A9S); and 18.0 m (A10S) (Figure 1). The letters S and T indicate the substrate over which the fixed quadrats were placed, sand and *T. testudinum*/*S. filiforme*, respectively. Twenty quadrats were placed in the protected zone. In the fished zone (B), quadrats were placed at 1.0 m (B1T–B1S) and 4.0 m, where two stations (B2T–B2S, B3T–B3S) were sampled. Six quadrats were placed in the fished zone.

Sampling was conducted with the aid of SCUBA, every 15 days for a period of 8 months from January 1981 and then monthly through May 1982. In each quadrat the total number of queen conchs and the shell length (Alcolado 1976) of each queen conch were determined and recorded.

The shallow DMS grassbed (AD) was divided into five strata, parallel to the coastline, and extended from it to a distance of approximately 50 m. Each stratum had a width of 10 m and a length of 60 m (Figure 1). The depths of the first three strata were approximately 0.2 to 0.4 m and increased in the furthest two (0.5 to 1.0 m). Because this seagrass bed was isolated from the others and the queen conchs in this area appeared to remain there over long periods of time, we had a good opportunity to study and analyze their population dynamics. Counts and measurements (shell length) were made monthly of all individuals in each stratum during the first 8 months from January 1981 and every 2 months through April 1983.

Once the reproductive season began (determined by migrations to shallow areas, observations of copulations, and presence of egg masses), counts were made of the number of egg masses found in each quadrat. The sampling was carried out every 15 days during the season until no egg masses were found. Because egg hatching takes from 4 to 6 days and an egg mass totally disappears in 9 to 13 days, the time interval between samples guaranteed that no egg mass was counted twice.

A daily record of water temperature was kept to establish possible relationships with reproductive activity.

The sex ratio of the queen conch population in the DMS grassbed was determined on two occasions: once in January 1981, 200 individuals (30% of the population) and again in July 1983, 100 individuals (40%) were sexed. In May 1983, the sex of 600 conchs was determined from a group of 2,000 conchs captured by local fishermen.

In June 1982, an experiment was conducted to estimate the number of viable egg masses that a female was capable of laying after mating. A 25-m^2 plastic corral (height, 40 cm; mesh width, 6 cm) was placed at a depth of 4.0 m on a sandy bottom with little cover of *T. testudinum*. Twenty-three (23) females, which were copulating or copulating and egg laying simultaneously, were collected from adjacent areas, tagged for individual identification, and placed in isolation inside the corral. Each female was observed daily. The number of egg masses laid by each female and the time taken to lay them were recorded. Egg masses in advanced stages (> 90% of the mean size) were taken to the laboratory, placed in 70 ℓ plexiglass aquaria with filtered sea water, and left to hatch to estimate viability. The temperature and salinity in the aquaria varied from 26.2° to 28°C and 37.5 to 38.0 ppt, respectively. Viability was qualitatively estimated by comparing veliger swimming activity and density (number of larve per litre).

To estimate the number of eggs in an egg mass, 30 egg masses were collected randomly during the reproductive season of 1982 from the 4.0- and 6.0-m sampling areas and taken to the laboratory where each was weighed (± 1 g)

and measured (length and width; ± 1 mm). From each mass, three fractions of arbitrarily different sizes, two at the extremes and one at the center, were measured, weighed, and introduced into a Clorox® solution (0.5%)for 5 minutes to remove adherent sand grains. The egg filament of each fraction was stretched and measured, and 10 counts of number of eggs · cm^{-1} were made. Thus, with the mean number of eggs cm^{-1}, the length of the filament, and weight of each fraction, the total number of eggs per egg mass was estimated.

To study queen conch migration, a tagging program was implemented. Every month all adults found at the fixed quadrats placed in the protected area (A) at depths of 4.0, 6.0 and 8.0 m (Figure 1) were tagged. The tag consisted of a steel wire attached to a numbered, plastic tag that was affixed to the whorl of the shell. One day after tagging, an area of approximately 7,000 m^2 surrounding each quadrat was examined. A total of 325 conchs were tagged in this area from March 1981 through October 1982. In addition, during the reproductive season of 1981, 114 conchs that had migrated into the shallow areas by the beach of Dos Mosquises-Sur were also tagged.

To estimate natural growth rate, 425 conchs with shell lengths between 3.0 and 19.0 cm were measured, tagged, and released in the DMS seagrass bed during 1981 and 1982. Their subsequent recapture and measurement provided growth-rate data.

To estimate mortality, a record was kept of the number of dead individuals (empty shells) and broken shells that were found during the regular sampling of the DMS grassbed. Attempts were made to identify the responsible predators by analyzing the type of breakage or perforation. In this and other grassbeds in the archipelago, many *in situ* observations were made on the activities of conch predators. Gut analyses were made of all of the fishes and invertebrates caught with a beach dragnet on shallow grassbeds during the day and night.

RESULTS

Queen conchs were widely distributed in the archipelago. They were most common in grassbeds of *T. testudinum*, *S. filiforme*, or mixed stands of both, and sandy bottoms with algal patches. Queen conchs were occasionally observed on sandy slopes at depths of 25 m and on reef slopes at 30 m. Adults of *S. gigas* were also found on the reef at depths ranging from 1.0 to 6.0 m, in areas formed mainly by the corals *A. cervicornis, M. annularis* and *S. siderea.* Queen conchs were also observed among the prop roots of the red mangrove *Rhizophora mangle* Linnaeus, on a sandy substrate with abundant plant detritus.

Although juvenile conchs were observed in many different habitats, they occurred most frequently in shallow grassbeds (0.1 to 1.0 m) and especially in the DMS grassbed.

The data on population density and shell length of queen conchs as a function of depth and averaged for the entire sampling period (January 1981 – May 1982) are summarized in Table 1. The mean population density was highest at depths of 4 to 8 m, and significantly ($p < 0.001$) higher in grassbeds of mixed stands of *T. testudinum* and *S. filiforme* (0.48 to 0.53 ind · m^{-2}) than in sandy substrates (0.24 to 0.43 ind · m^{-2}). The highest densities occurred at stations in 4.0 m (0.46 ind · m^{-2}) with predominance of adults with a mean shell length of 21.2 cm (± 1.17). The mean population density decreased and mean shell length increased with increasing depth, with the exception of the 6.0-m station where a high proportion of juveniles was found (Table 1). Conchs with the greatest mean shell length occurred at the deepest station (19.0 m) over sandy substrate. The variance of mean shell length decreased with depth suggesting that, in deeper areas, the population was more homogeneous in terms of shell length (age) (Table 1). In the fished zone (B) the mean population density (0.08-0.09 ind · m^{-2}) and mean shell length (17.7-18.6 cm) did not vary with depth and were significantly lower than the values estimated for the unfished zone ($P < 0.01$) (Table 1). A comparison of the distributions of shell length frequencies of queen conch populations between unfished (A) and fished (B) zones clearly shows the lack of adults and the predominance of juveniles in the latter areas (Figure 2). Monthly variations in population density in these zones were minimal.

In the DMS grassbed the mean density was 0.23 ind · m^{-2}, although densities of 2.1 ind · m^{-2} usually occurred. The population in this bed consisted primarily of juveniles (Figure 3) with shell lengths ranging from 2.1 to 16.0 cm. Juveniles were found aggregated, usually burrowed, in sand patches during the day and at low tides. Conchs were most abundant in the strata closest to shore (Table 1, Figure 4A). Monthly changes in conch abundance in each stratum were high and primarily reflected the massive mortality that occurred during April–June 1981, when extremely low tides eliminated approximately 76% of the population (Figure 4B). Conch movements from the shallow to the deeper strata and back in response to changes in tide levels may also explain variations in the monthly abundance curves (Figure 4A, 4B); at low tides the greatest abundance occurred in the stratum furthest from the coastline and vice versa (Figure 5).

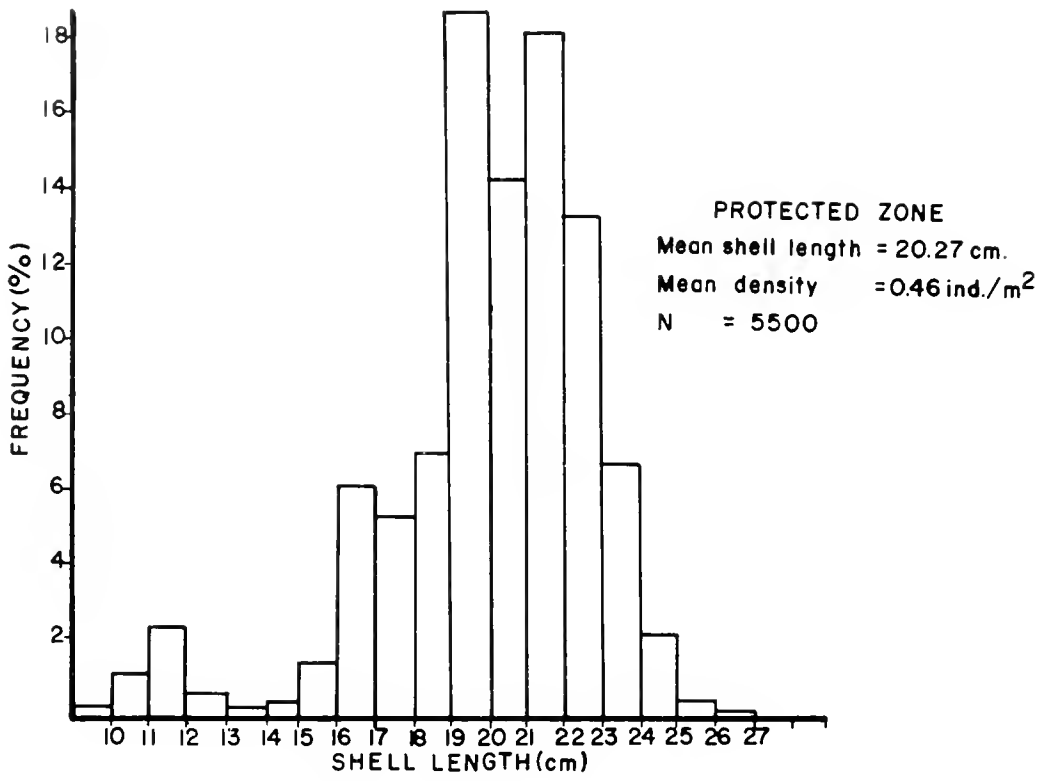
The results of the tagging program were not conclusive because of the low rate of recaptures; thus definite migration and movement patterns could not be determined. It was notable, however, that none of the 325 tagged conchs in the fixed quadrats at depths of 4.0 to 6.0 and 8.0 m in the protected zone (A) were found in an area of 7,000 m^2 around each quadrat within 24 hours of tagging. Only two of the tagged conchs were recaptured during the 2-year study; one, a month after tagging at about 1 km away, and the other 3 months later approximately 2 km away. Of the 114 tagged conchs that were released in the shallow areas by the beach of Dos Mosquises, only 3 were recaptured;

TABLE 1.

Summary table of mean density and shell length of queen conchs *Strombus gigas* found at different sampling sites in the Archipiélago de Los Roques National Park from January 1981 through May 1982.

Area	Depth m	Station Code	Substrate Type*	Mean Density ind · m^{-2}	Maximum Density ind · m^{-2}	Minimum Density ind · m^{-2}	Standard Deviation ind · m^{-2}	Mean Shell Length cm	Maximum Shell Length cm	Minimum Shell Length cm	Standard Deviation cm	Overall Mean Density ind · m^{-2}	Standard Deviation ind · m^{-2}	Overall Mean Shell Length cm	Standard Deviation cm
PROTECTED	1.0	A1T	T	0.19	0.48	0.08	0.12	18.5	22.9	16.0	3.06	0.15	0.12	18.8	3.20
		A1S	S	0.10	0.40	0.0	0.13	19.0	22.5	12.3	3.34				
	4.0	A2T A3T A4T	T	0.51	0.92	0.32	0.19	20.91	23.4	19.3	1.21	0.46	0.16	21.0	0.97
		A2S A3S A4S	S	0.41	0.60	(0.16)	0.13	21.12	23.0	18.7	0.72				
	6.0	A5T A6T	T	0.53	1.08	0.08	0.22	18.9	21.9	11.6	2.67	0.39	0.18	19.30	0.97
		A5S A6S	S	0.24	0.60	0.08	0.13	19.7	22.4	12.0	2.71				
	8.0	A7T	T	0.43	0.60	0.10	0.84	20.20	22.7	19.3	0.84	0.35	1.18	20.3	0.77
		A7S	S	0.26	0.68	0.04	1.52	20.33	22.9	19.5	0.70				
	12.0	A8S	S	0.06	0.16	0.0	0.05	20.70	22.9	19.5	0.70	0.06	0.05	20.7	0.70
	15.0	A9S	S	0.04	0.24	0.0	0.07	21.0	23.2	20.0	0.60	0.04	0.07	21.0	0.60
	18.0	A10S	S	0.03	0.32	0.0	0.08	21.9	23.8	21.0	0.54	0.03	0.08	21.9	0.54
	0.10	AD-1	T	0.37	0.60	0.07	0.15	14.83	28.4	2.1	2.7	0.23	0.04	17.32	1.7
	0.10	AD-2	T	0.34	0.50	0.09	0.11	16.49	28.4	5.4	0.9				
	0.15	AD-3	T	0.31	0.48	0.06	0.16	17.89	28.3	5.6	1.3				
	0.30	AD-4	T	0.13	0.32	0.001	0.10	19.84	29.7	9.5	1.6				
	0.50–1.0	AD-5	T-S	0.04	0.07	0.0	0.02	19.74	29.3	11.3	1.8				
FISHED	1.0	B1T	T	0.16	0.24	0.0	0.09	15.9	19.4	13.6	1.08	0.09	0.07	16.85	1.02
		B1S	S	0.01	0.09	0.0	0.01	17.8	20.4	15.3	0.96				
	4.0	B2T B3T	T	0.17	0.32	0.02	0.11	16.68	17.6	15.8	0.72	0.09	0.11	17.40	1.86
		B2S B3S	S	0.02	0.06	0.00	0.02	18.00	22.3	13.7	1.87				

*Substrate Type: T, *Thalassia testudinum;* S, sand



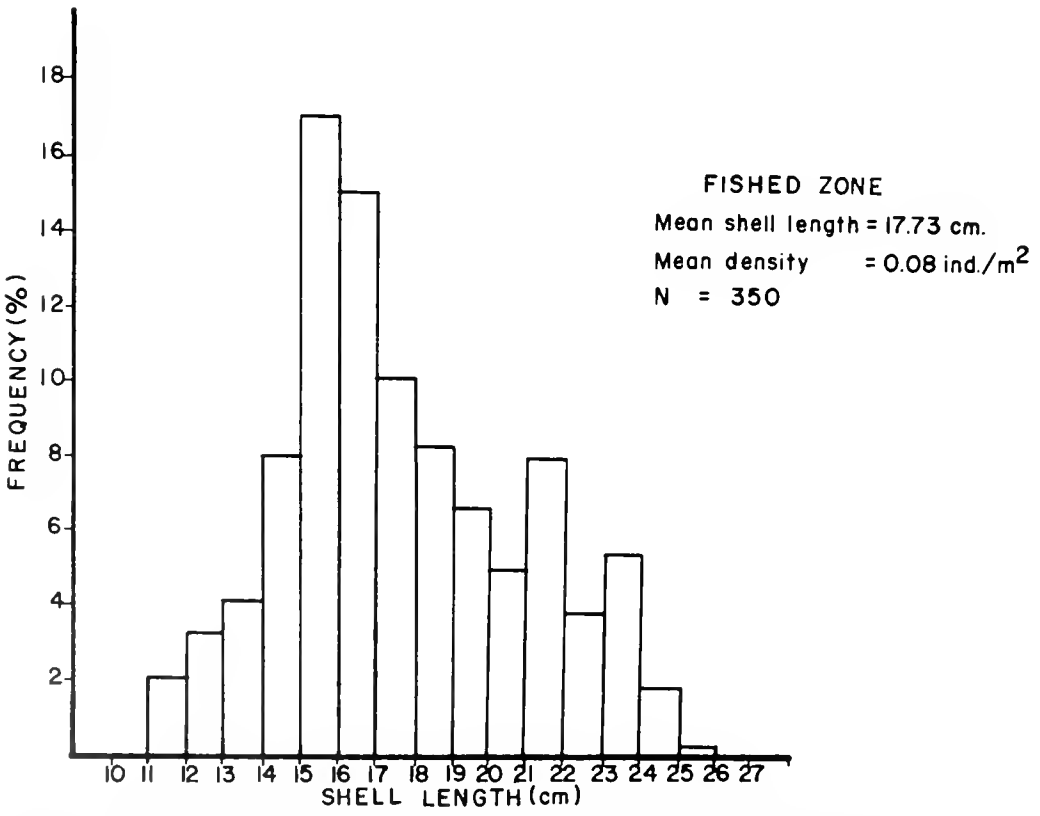


Figure 2. Comparison of the distributions of shell-length frequencies of queen conchs between the protected and fished zones. Data for the entire sampling period (January 1981 – May 1982) were pooled.

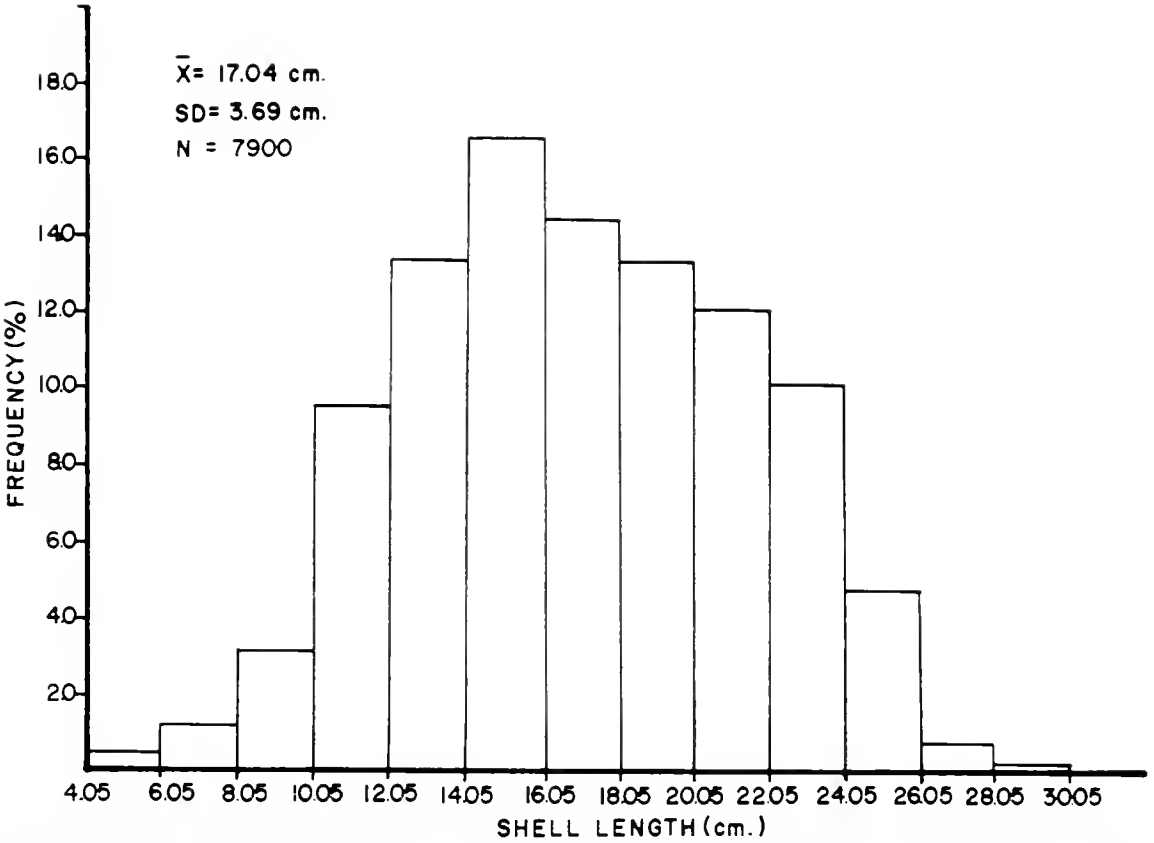


Figure 3. Shell-length frequency distribution of queen conchs in the shallow Dos Mosquises-Sur (DMS) grassbed (AD, Figure 1). Data for the entire sampling period (January 1981 through May 1982) were pooled.

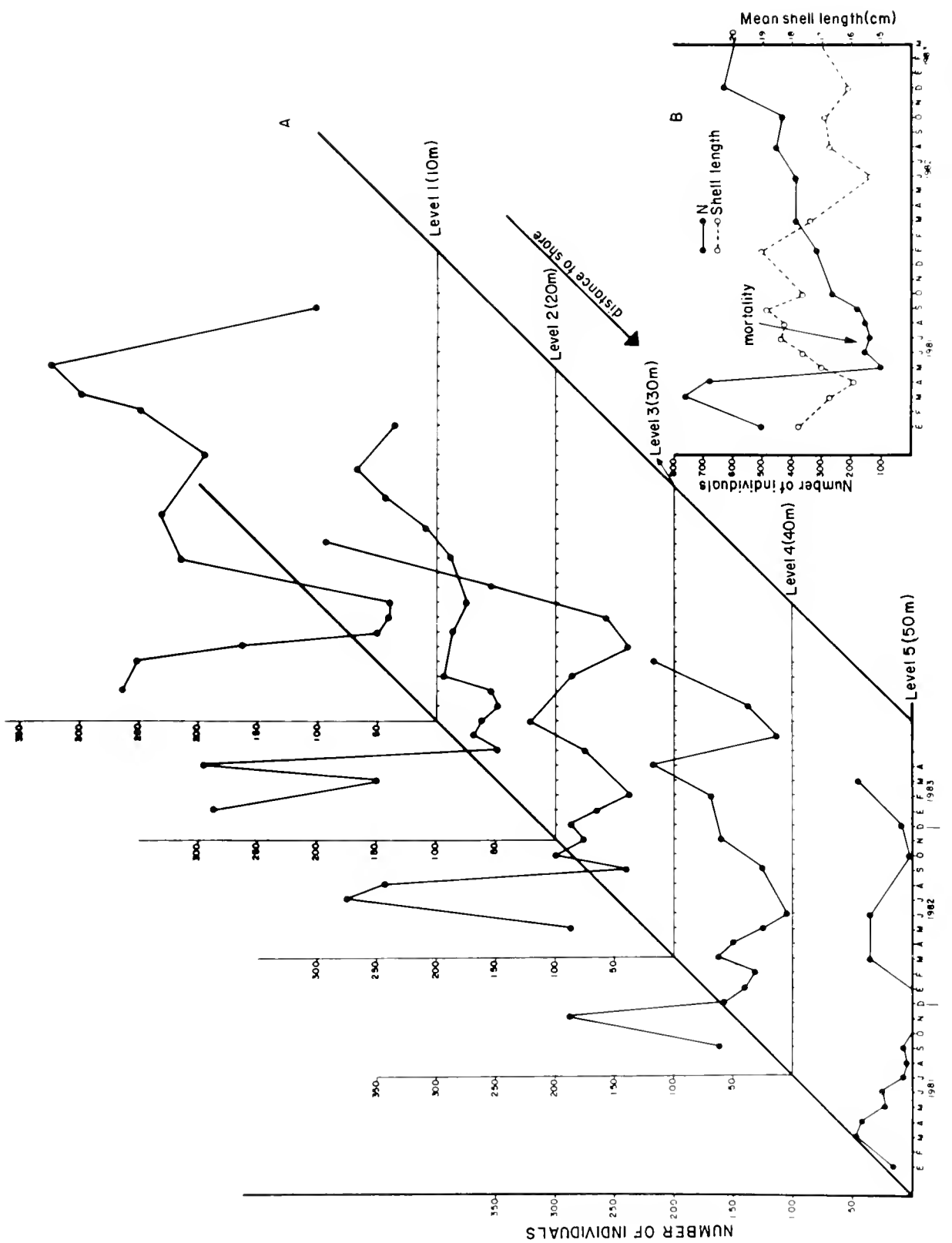


Figure 4. (A) Monthly abundance of queen conchs by strata in the shallow Dos Mosquises-Sur (DMS) grassbed (AD, Figure 1) for the period January 1981 through May 1983; (B) total queen conch abundance and mean shell length by month for the entire grassbed for the same time period.

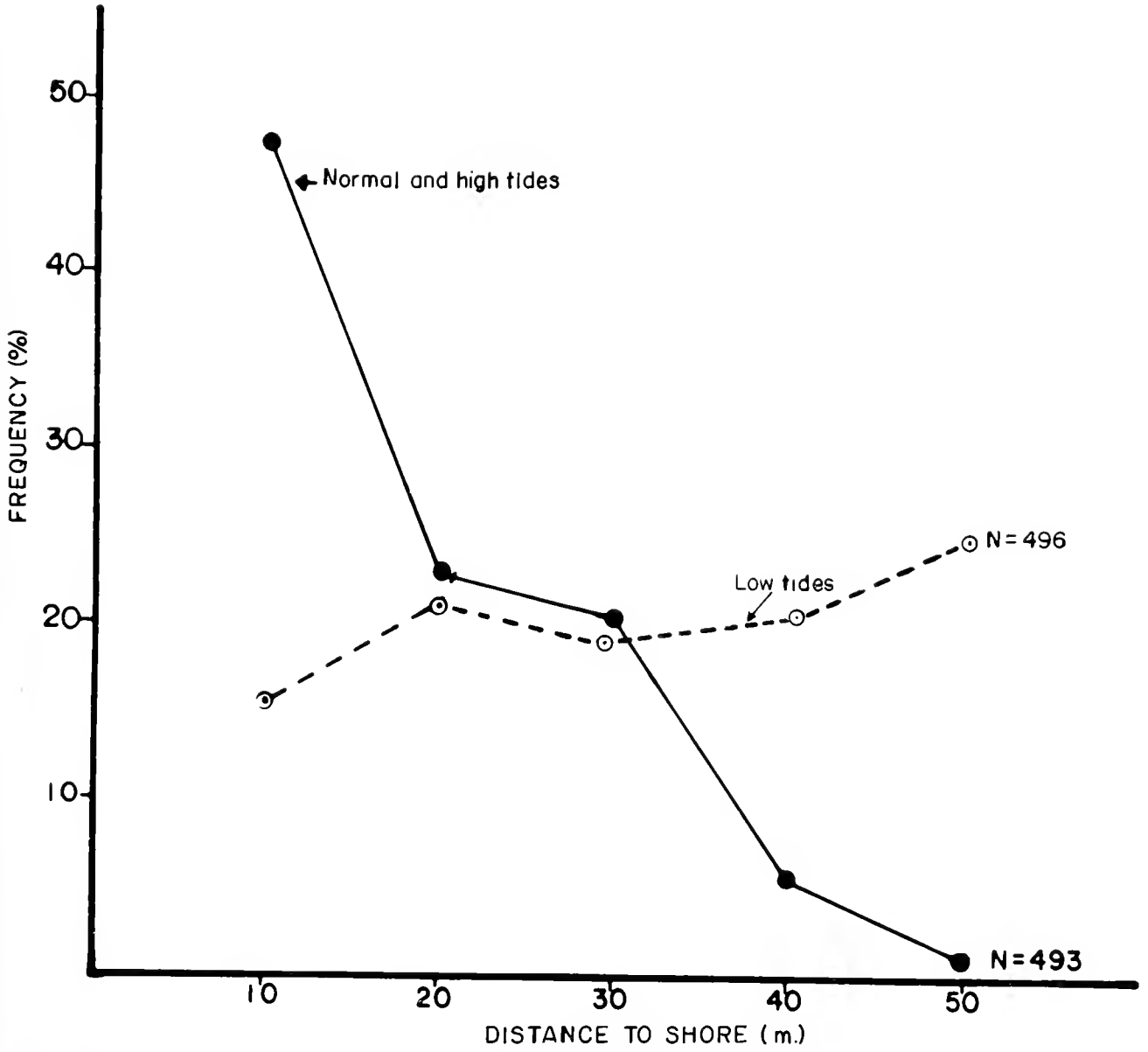


Figure 5. Relationship between queen conch frequency and distance to shore at two tide levels in the Dos Mosquises-Sur (DMS) grassbed (AD, Figure 1).

all 3 in the grassbed in the protected zone (A) (Figure 1) within a distance of 1 km.

The conch reproductive season began by the end of April as indicated by increased migratory activity (movement to shallow and sandy areas) and reproductive aggregations with isolated copulations. A delay of approximately 15 days occurred between this time and the time that the first egg mass was found in May.

A high correlation was found between the initiation of reproductive activities and rising water temperatures (with a 3°C annual variation of temperature at the surface) (Figure 6A, 6B). In both 1981 and 1982, the peak in reproductive intensity, as expressed in terms of number of egg masses · m^{-2} of substrate, occurred in August and September at times of highest water temperatures.

The reproductive season ended by late October and November at times of decreasing water temperatures; however, in 1981, egg masses were found through December 15 in very shallow areas (DMS grassbed). In shallow areas the reproductive activities began a month later than in deeper areas (June). In 1982, water temperatures began to increase a month later than in 1981 and, consequently, the reproductive intensity was delayed correspondingly (Figure 6A, 6B). A slightly higher proportion of egg masses was laid over sand with an abundant cover of the following algal species: *Laurencia papilosa* (Forsskal), *Dyctiota dichotoma* (Hudson), *D. divaricata* Lamouroux, *Halimeda monile* (Ellis and Solander), *H. discoidea* Decaisne, and *H. opuntia* (Linnaeus). Up to 8 masses · m^{-2} of substrate were occasionally found on sand patches.

The sex ratio of the queen conch populations sampled was 1:1.

Of the 15 females that were mating prior to isolation in the 25-m^2 submarine corral, 3 laid six egg masses, 4 laid four egg masses, and 8 laid one to three egg masses apiece. The mean time interval between successive egg layings was 8.6 (± 4.0) days (Table 2). Of the 22 females that were mating and laying eggs simultaneously prior to isolation, 2 laid six egg masses and 20 laid one to three egg masses apiece at similar time intervals. Overall, the mean interval between successive egg depositions was 8.7 (± 4.9) days. If reproduction continues throughout the breeding season, as evidenced by females which were frequently observed copulating and laying eggs at the same time, then each female could lay 4.0 egg masses per month. That rate amounts to a deposition of 25 egg masses during a reproductive season.

The qualitative viability tests which were conducted on all of the egg masses laid by 10 isolated females (to prevent further copulation) showed that the first 3 to 4 egg masses were fully viable with normal hatching (veliger density 300 · ℓ^{-1}) and veliger activity. The viability of the last 3 to 6 masses was very low as indicated by the low density of veligers (< 50 · ℓ^{-1}). The last egg masses were slightly smaller than the first 3 to 4.

The total number of eggs contained in an egg mass was estimated. The mean number of eggs along a filament was 120.5 ± 5.39 · cm^{-1}. The total length of the filament of a fraction varied proportionally according to its weight. For example, a fraction with a weight of 12.0 g had a filament length of 350 cm and, thus, approximately 42,000 eggs. With these relationships the total number eggs per mass was estimated; a high and significant correlation ($r = 0.95$, $p < 0.01$) was found between the fresh weight of an egg mass and the total number of eggs (Figure 7). For example, the average cleaned egg mass of 100 g (fresh weight) had a filament length of 2,460 cm and approximately 405,000 eggs.

In the DMS grassbed (3,000-m^2 area) the mortality rate from predation was estimated at 1.3 ind · mo^{-1}. The primary predators in this area were the spiny lobster *Panulirus argus* Latreille, the porcupinefish *Diodon hystrix* Linnaeus, the common Atlantic octopus *Octopus vulgaris* Cuvier, and the southern stingray *Dasyatis americana* Hildebrand and Schroeder. If deaths from dessication are included, the mortality rate was 2.08 ind · mo^{-1}; the deaths recorded during the massive mortality of April–June 1981 were not included in this estimation. During that period, extremely low tides in conjunction with low wind speeds (2.0 m · sec^{-1}) and relatively little cloud cover which lasted about 5 h · day^{-1} for 10 days eliminated 76% of the entire population. This event reduced the conch density from 0.26 to 0.07 ind · m^{-1} (Figure 4A and 4B). During those 10 days, most (80%) of the grassbed, especially the area adjacent to the coast line, was exposed to air and direct sunlight. In a few shallow tidal pools temperature and salinity rose to 36°C and 41 ppt, respectively. After that phenomenon, the recovery rate of the population from immigration and recruitment was approximately 28 ind · mo^{-1} (Figure 4B). Conch abundances reached the pre-April 1981 level after two years.

In deeper areas, the mortality rate could not be estimated; however, heavy predation on conchs was observed. The most common predators observed were large and small hermit crabs, *Petrochirus diogenes* (Linnaeus), spotted stingrays, *Aetobatus narinari* (Euphrasen), large stingrays *D. americana*, gastropod molluscs like the true tulip *Fasciolaria tulipa* (Linné) and the trumpet triton *Charonia variegata* (Lamarck). Other predators which were occasionally observed included the spotted moray *Gymnothorax moringa* (Cuvier), juveniles of the green moray *G. funebris* Ranzani, juveniles of the common octopus *O. vulgaris* and the apple murex *Murex pomun* Gmelin.

Juveniles which had a shell length of < 4 cm were never observed in the areas sampled or in approximately 400 sediment samples. Thus, it was difficult to evaluate the real intensity and periods of recruitment. The appearance of juveniles with a shell length between 4 and 8 cm was, therefore, considered as "recruitment." Thus, with the data on growth rates in nature (0.9 cm · mo^{-1}) and time taken for larval development (20 to 35 days) (Laughlin

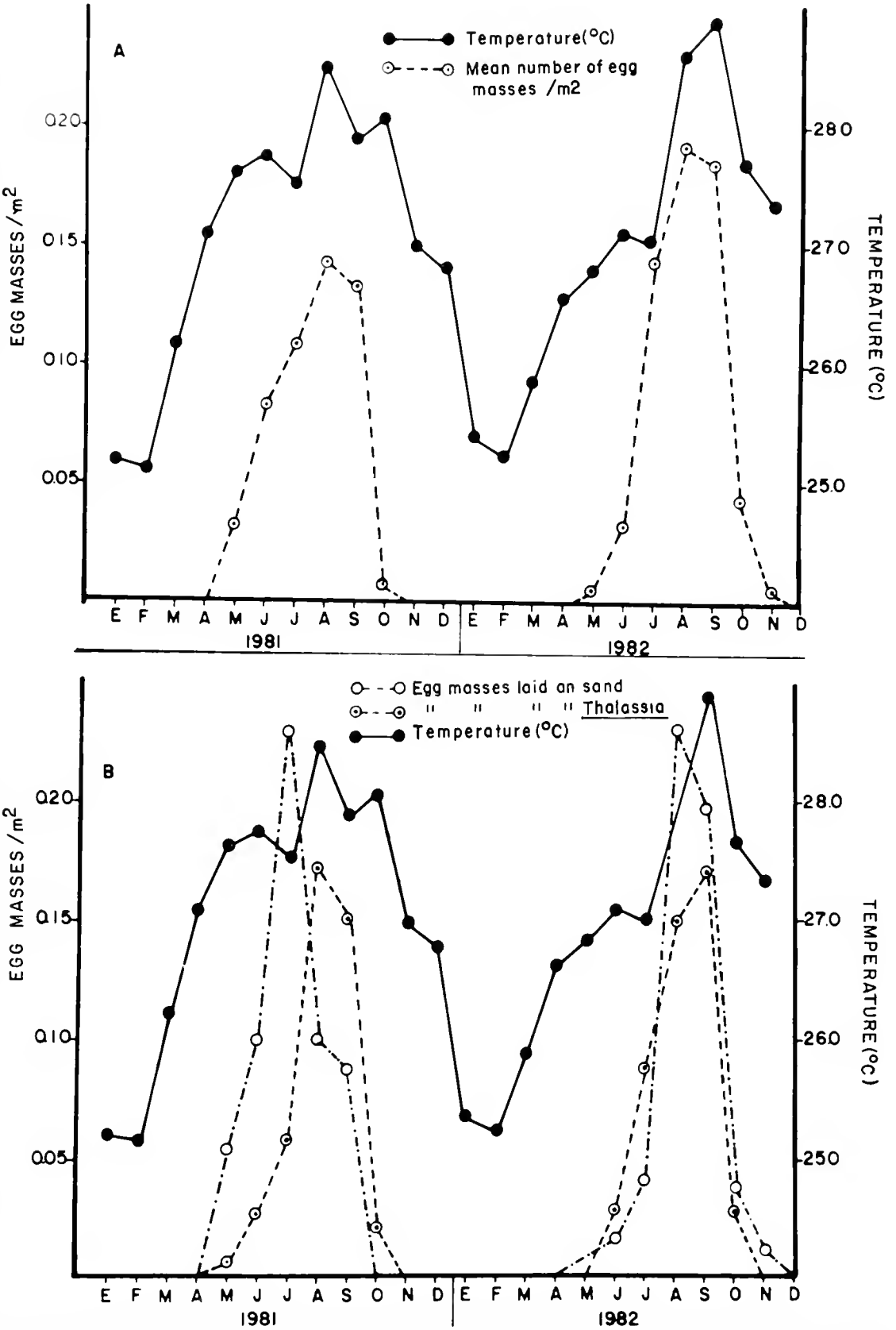


Figure 6. (A) Mean monthly variations in density of queen conchs, egg masses, and water temperature for all stations pooled; (B) Monthly variations in density of egg masses laid over sandy and grassbed (*Thalassia testudinum*) substrates.

TABLE 2.

Summary of the time intervals (days) between subsequent egg layings by tagged female queen conchs isolated in a submarine corral.

Identifying Number	Behaviour Observed*	Date of Introduction into the Corral	Number of Subsequent Egg Layings (days between egg layings)					
			1	2	3	4	5	6
1947	C O	07/22/82	10	9				
1950	C	07/25/82	3					
1952	C	06/23/83	5	6	4	15		
1953	C O	06/23/83	13	7	10			
1954	C	06/23/83	5	6	20	15		
1956	C	06/18/83	5	12	22	3	10	7
1957	C	06/18/83	4	7	7			
1958	C	06/18/83	6	7	9			
1959	C	06/16/82	5	14	18			
1960	C	06/23/82	5	6	14	9		
1961	C O	09/02/82	7	6				
1967	C O	07/22/82	6					
1968	C O	07/22/82	3	13	7			
1969	C O	09/02/82	9	4	8			
1975	C	06/17/82	6					
1976	C	06/18/82	5	6	8			
1979	C	06/23/82	5	6	4	14		
1980	C O	09/23/82	8					
1981	C	06/23/82	4	7	7	7	5	7
1982	C O	06/23/82	4	7	7	9	4	22
1989	C	06/23/82	5	8	3	14	6	11
1990	C O	09/23/82	12	8				
1991	C	06/17/82	6	5	8			
1992	C	06/17/82	6	13	18			
1994	C O	06/17/82	5	6	3	10	15	8
		$\bar{X}$:	6.08	7.76	9.83	10.66	8.0	11.00
		Sx:	2.53	2.82	5.97	4.15	4.52	6.36

*C, copulating; O, egg laying; CO, copulating and egg laying simultaneously

and Weil 1983) the periods of real recruitment were estimated. The juveniles with shell lengths between 4 and 5 cm probably reached the grassbed 5 to 7 months earlier, and juveniles of 6 to 8 cm settled 8 to 10 months earlier. Therefore, the recruitment of larvae or early juveniles must have occurred primarily between June and September (Figure 8).

The low emigration rate of tagged conchs from the DMS grassbed resulted in the recapture of a high percentage (> 90%) of those individuals during monthly samples. The natural growth rate of 130 individuals varied from 0.4 to 1.5 cm in shell length per month, with a mean of 0.9 (± 0.2) cm · mo^{-1} (Figures 9 and 10). When a juvenile approaches adult size (which can vary from a shell length of 18.0 to 26.0 cm), its labium or outer lip begins to grow until the complete development of a thin lip is reached, which takes about 3 months (Figure 10). It takes approximately 2 more months for the juveniles to reach sexual maturity after which the labia and the rest of the shell are thickened by the deposition of calcium carbonate. Subsequently, shell length growth ceases as indicated on Figures 9 and 10.

DISCUSSION

In Los Roques queen conchs were most abundant in very shallow areas that were exposed during extremely low tides and in grassbeds of *T. testudinum* and *S. filiforme* at depths ranging from 4 to 8 m; they were less abundant in deeper grassbeds, and on sandy slopes and coral reefs down to depths of 30 m. Brownell (1977) found queen conchs in this locality at depths of 40 m, and Alcolado (1976) reports the same maximum depth for conchs in Cuba. Their depth-dependent distribution appeared to be related to food availability, especially that of the epiphytes of *T. testudinum*, which constitute the primary diet of this species in Los Roques (De Santis 1982).

The variations in population density between the protected and fished areas clearly indicate that the latter is being subjected to intense fishing pressures. Further, the comparison of the shell length-frequency distributions of conch populations between the fished and unfished zones clearly shows the detrimental effects of overfishing; the large juveniles and adults have practically disappeared from the unprotected zone.

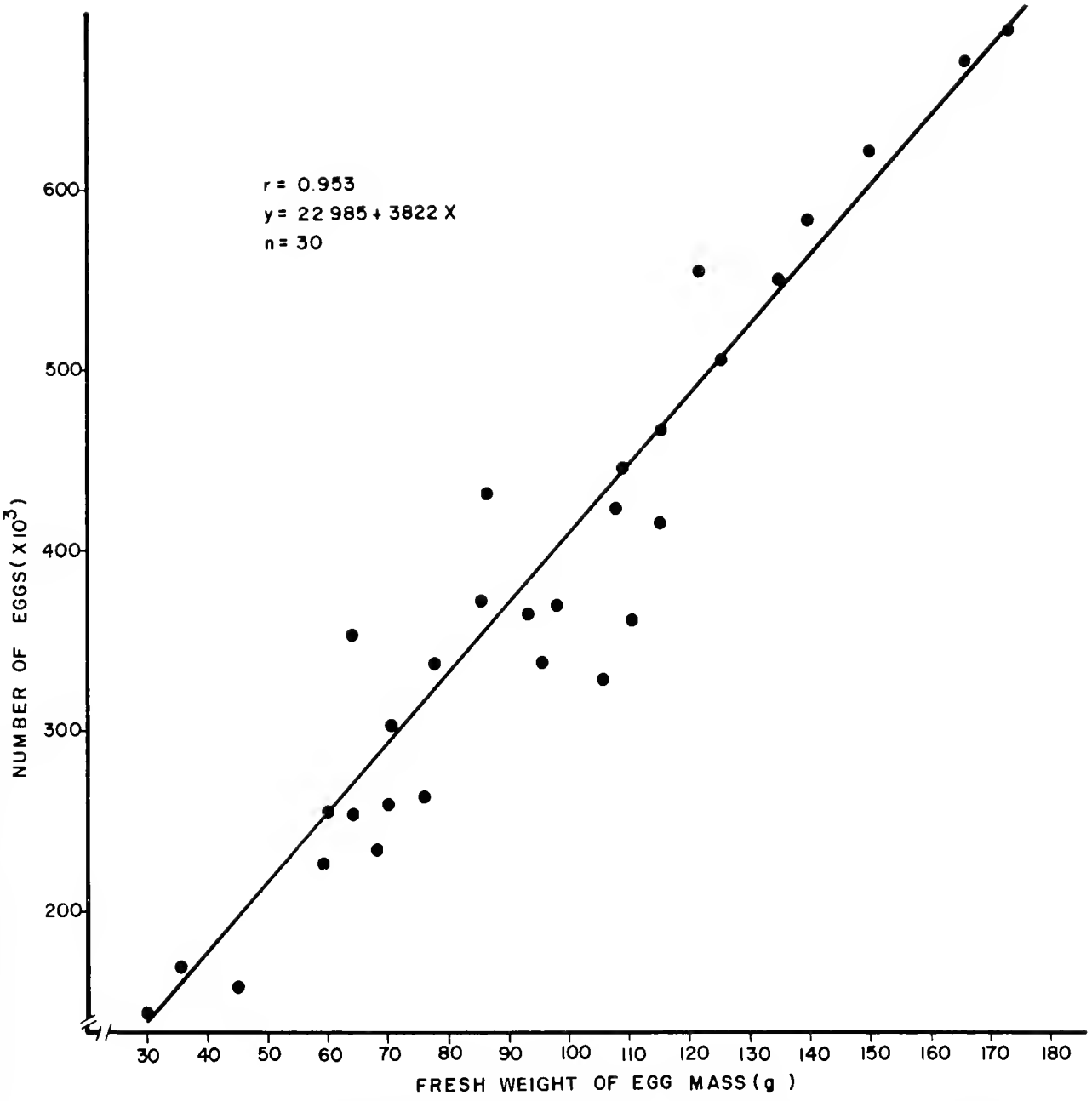


Figure 7. Relationship between fresh weight of an egg mass (g) of queen conchs and the total number of eggs.

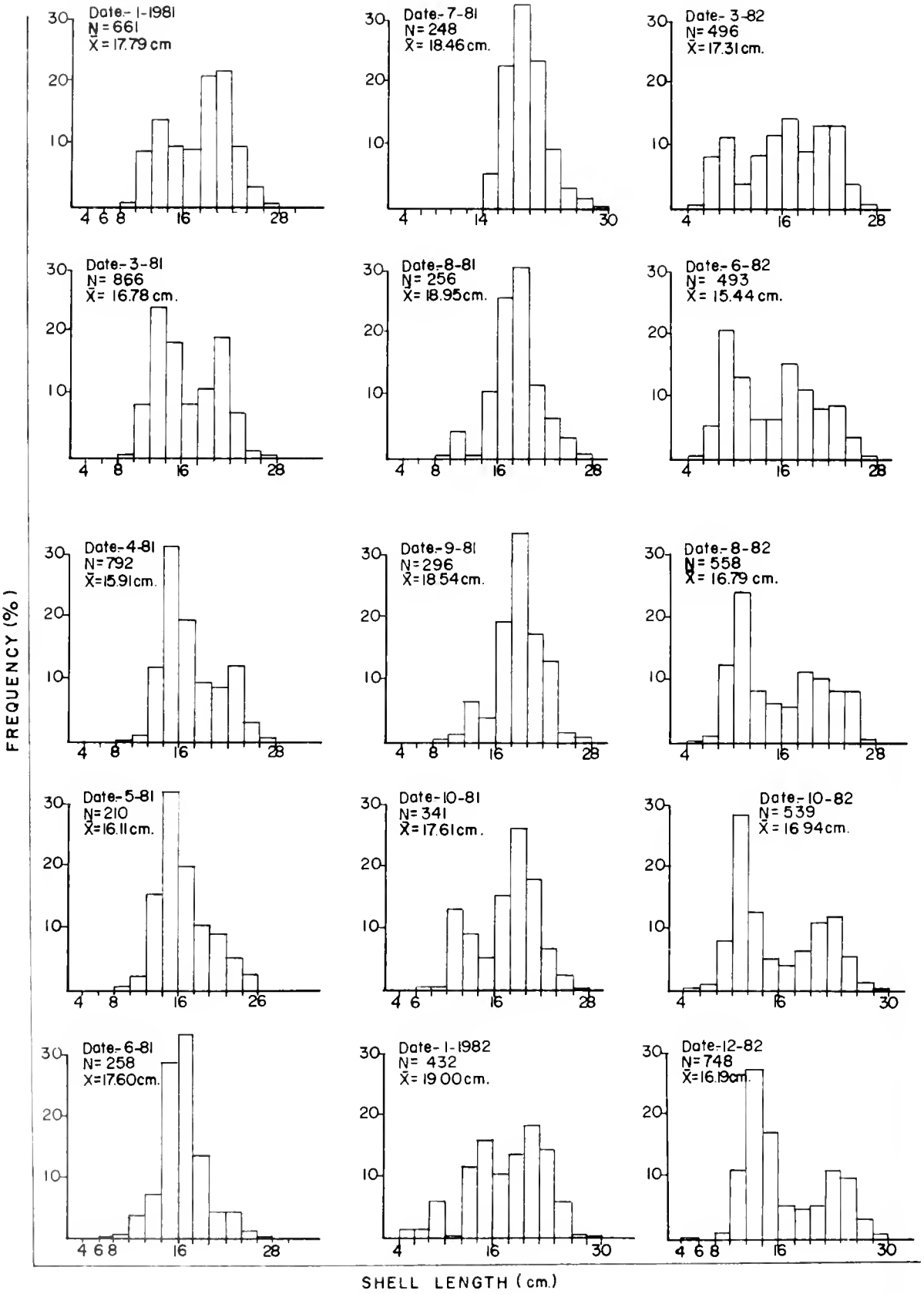


Figure 8. Monthly distribution of shell-length frequencies for queen conchs in the Dos Mosquises-Sur (DMS) grassbed (AD, Figure 1) from January 1981 through December 1982.

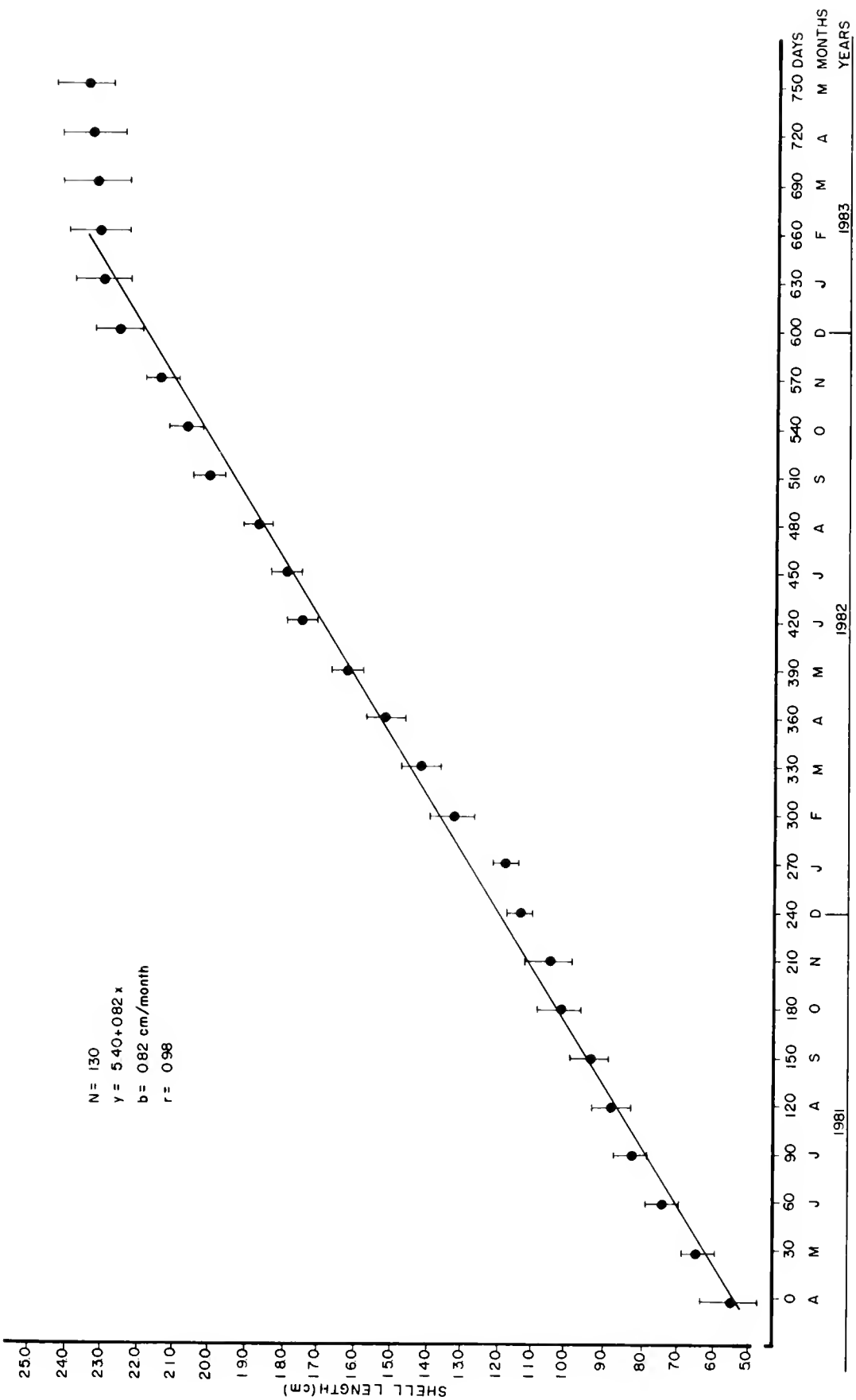


Figure 9. Growth in nature of 130 queen conchs from April 1981 through May 1983. Each queen conch was tagged for individual identification and shell-length measurement.

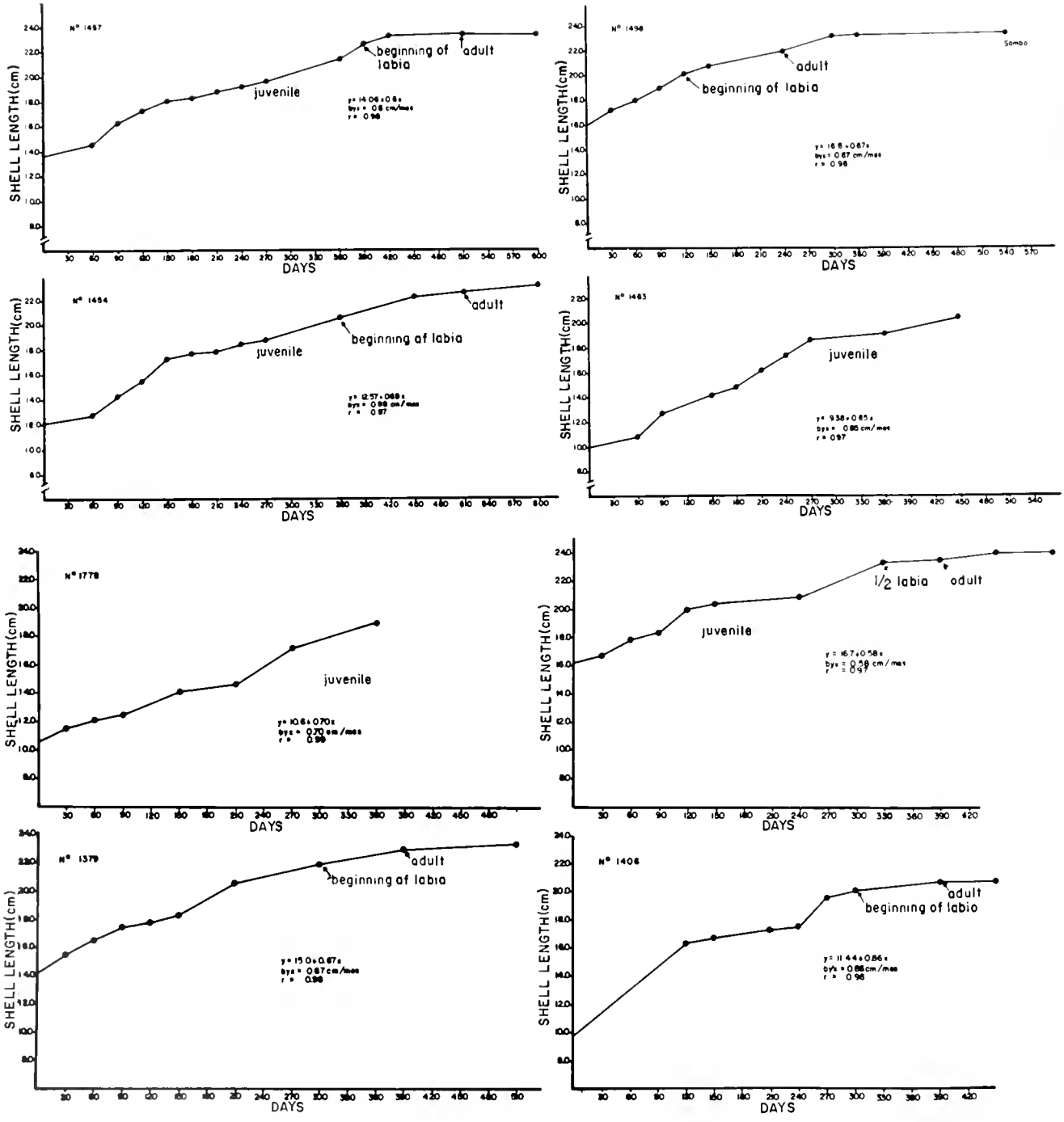


Figure 10. Examples of eight growth curves for tagged queen conchs in the Dos Mosquises-Sur (DMS) grassbed (AD, Figure 1).

Queen conch densities in the unfished zone could be considered natural when there is no fishery. In Cuba, Alcolado (1976) found that natural population densities of conchs varied between 0.04 and 0.9 ind · m^{-2} with mean values comparable to those estimated in this study. The high densities of up 2.1 ind · m^{-2} found in the shallow DMS grassbed were not common and, indeed, did not occur at any other areas of Los Roques. This finding could reflect the fact that there is no fishery in this area and that those types of grassbeds, which are located perpendicular to the direction of water currents, experience a partial stagnation of water and which possess abundant food resources, are ideal habitats for recruitment and growth of juvenile queen conchs. In fact, the population in such a bed consisted primarily of juveniles which aggregated in the northern section of the bed where currents were greatly reduced. Although this section of the bed was exposed during low tides, the juveniles were generally not affected because of their ability to burrow.

The increments in mean shell length and reduction of variance of this mean with increasing depth indicate that in deeper areas the queen conch populations consist primarily of adults of comparable shell length. The reverse was true for shallow grassbeds, although the largest conch (29.7 cm, shell length) was found in this area. That conch was about 6.0 cm longer than the largest queen conch reported by Alcolado (1976) for Cuba and comparable in size to that reported by Clench and Abbott (1941) as the maximum size for *S. gigas*.

Monthly changes in conch abundance and/or density were minimal in all areas except for the DMS grassbed where a massive mortality and subsequent recruitment influenced the abundance curve. In this bed, the month-to-month changes in abudance appeared to result from local movements to and from deeper strata in response to changes in tide levels rather than in response to temperature variations (Figure 5).

Although the tagging conducted in grassbeds at intermediate depths (4 to 8 m) did not yield significant results in terms of the number of conchs recaptured (thus eliminating the possibility of tracing definitive conch movement and migration patterns in this area), it did show that in large grassbeds adult conchs move considerably in terms of distance and frequency. Similar results were obtained by Hesse (1979). This, plus the fact that adult conchs were observed in a constant day-long feeding activity, appears to indicate that their feeding behavior resembles that of a "harvester," cropping a given area and then moving to the next. This behavior may explain why tagged conchs were never found in an area equivalent to 7,000 m^2 within 24 hours of tagging. The only traceable movement or migration observed occurred early in the reproductive period when large numbers of conchs moved from deeper grassbeds to shallow, sandy areas, probably in response to changes in water temperature and/or to the selection of appropriate grounds for egg laying. Such movements have been reported in the literature (Robertson 1959, Randall 1964, Hesse 1979). Results also showed that juvenile conchs are residents, move very little and remain in restricted areas (within 100 m^2) for long periods of time ($>$ 1 year).

Brownell (1977) found that the reproductive season of queen conchs in Los Roques extended from July through November. Our data indicated that the season extended from mid-April to November and appeared to be controlled by changes in water temperature, although those changes were relatively minor. Randall (1964) found that in the Virgin Islands conch reproduction ended in November or early December and resumed again in late January or in February or March. He suggested that temperature appeared not to be a controlling factor because if it was, a shorter spawning season would have occurred in the Virgin Islands and other northern areas, and year-around reproduction should occur in warmer regions such as Los Roques. Indeed, it was very surprising that the spawning season at Los Roques was shorter than in areas at higher latitudes.

Female conchs in Los Roques were capable of laying about 25 egg masses per season. Davis and Hesse (1983) reported a mean of 1 to 3 egg masses per queen conch per month in the Turk and Caicos Islands which represents a reproductive potential three times less than in Los Roques. This difference in reproductive potential between the Turk and Caicos Islands and Los Roques may reflect higher densities of conchs in the latter region and thus greater availability of males; and/or, perhaps the ambient conditions at Los Roques were more constant and favorable for reproduction.

The viability tests, which were conducted on egg masses laid by conchs in isolation, indicated that females were capable of maintaining the male's sperm alive for a period of about 25 to 30 days and, thereby, lay four viable egg masses apiece.

The greatest densities of egg masses were found at the 4- to 8-m depth range. Those densities decreased significantly in deeper and shallower areas. That pattern appeared to be a function of conch population density. In some areas, up to eight egg masses · m^{-2} were found and similar values have been reported for other areas in the Caribbean (Randall 1964, Davis and Hesse 1983).

Although data on reproductive behavior were not available for Los Roques, some behavioral patterns were observed that appeared to signal the initiation of reproduction. Conchs migrate toward shallow areas in early April and their mating frequencies increase toward July and August. On occasion, up to eight males were found with one female. Egg-laying females appeared to attract more males than mating females. That differential attraction plus the fact that males orient parallel to the direction of the current suggest that females may excrete a pheromone when laying eggs. On many occasions we observed females

depositing egg masses and copulating at the same time; this corroborates the findings of Randall (1964) and Davis and Hesse (1983).

Recruitment of metamorphosing juveniles occurs year around with peak values in the warmer months. Recruitment in the shallow DMS grassbed was very high following the massive conch mortality in April 1981. In fact, after the massive mortality, the population level recovered within a period of 2 years for a recovery rate of 28.1 ind $\cdot$ mo^{-1} in an area of 3,000 m^2. Although this value included the adult immigrations, it appeared to be insignificant when compared to larval recruitment which was determined by the appearance of small juveniles.

The monthly growth rate of queen conchs in the field at Los Roques was high (0.4 to 1.5 cm $\cdot$ mo^{-1}) and comparable to that Alcolado (1976) reported for Cuba. Laughlin and Weil (1983) compared natural and laboratory growth rates at Los Roques. At a growth rate of 0.6 cm $\cdot$ mo^{-1}, a period of 3 years is required for a recently metamorphosed queen conch to reach a minimum commercial size of 20 cm (shell length).

Based on these results and the fact that natural mortality is low and the reproductive potential of conchs appears to be extraordinarily high, we believe that in the Los Roques archipelago the natural repopulation of overfished areas can occur in a very short period of time. That repopulation rate will occur only if fishing is prohibited in key areas around the archipelago, as is the case for the areas surrounding Dos Mosquises.

ACKNOWLEDGMENTS

We thank the staff of the Dos Mosquises Marine Station for their help throughout the project and the Laboratory of Photography of the Faculty of Science, Universidad Central de Venezuela for the photographic reproduction of the drawings. We are especially grateful to Drs. Scott Siddall, Roger Mann and Edwin Cake for critically reviewing the manuscript, and to Margot Grillo, José Marval, Pablo Rodríguez, Javier Ruíz, Francisco Pulido, Alicia Ochoa and Miguel Hauschild for their assistance in the field.

This project was financed by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT) by grant number S1–1182.

REFERENCES CITED

Alcolado, P. M. 1976. Crecimiento, variaciones morfológicas de la concha y algunos datos biológicos del cobo *Strombus gigas* L. (Molusca; Mesogastropoda). *Acad. Cienc. Cuba Ser. Biol.* 33 p.

Brownell, W. N. 1977. Reproduction, laboratory culture and growth of *Strombus gigas, S. costatus* and *S. pugilis* in Los Roques, Venezuela. *Bull. Mar. Sci.* 27:668–680.

_____ & T. Stevely. 1981. The biology, fisheries and management of the queen conch *Strombus gigas. U.S. Natl. Mar. Fish. Serv., Mar. Fish. Rev.* 437:1–12.

Clench, W. J. & R. T. Abbott. 1941. The genus *Strombus* in the Western Atlantic. *Johnsonia* 1:1–15.

Davis, M. & C. Hesse. 1983. Third world level conch mariculture in the Turk and Caicos Islands. *Proc. Gulf Caribb. Fish. Inst.* 35:73–82.

De Santis, C. 1982. Algunos aspectos de la ecología trófica del botuto, *Strombus gigas,* en el Archipiélago de Los Roques. Trabajo Especial de Grado, Universidad Central de Venezuela. 84 p. [Thesis]

Hesse, K. D. 1979. Movement and migration of the queen conch, *Strombus gigas* in the Turk and Caicos Islands. *Bull. Mar. Sci.* 29:303–311.

Laughlin, R. A. 1983. Cultivo del botuto *Strombus gigas.* Cervigón, F., editor, *La Acuicultura en Venezuela: Estado Actual y Perspectivas.* Caracas, Venezuela: Editorial Arte; p. 46–48.

_____ & E. Weil M. 1983. Queen conch mariculture and restoration in the Archipiélago de Los Roques: Preliminary results. *Proc. Gulf Caribb. Fish. Inst.* 35:64–72.

Randall, J. E. 1964. Contribution to the biology of the queen conch, *Strombus gigas. Bull. Mar. Sci. Gulf Caribb.* 14:246–295.

Robertson, R. 1959. Observations on the spawn and veligers of conch (*Strombus*) in the Bahamas. *Proc. Malacol. Soc. Lond.* 33:164–172.

Journal of Shellfish Research, Vol. 4, No. 1, 63–66, 1984.

QUANTIFICATION OF THE DENSITY–GROWTH RELATIONSHIP IN HATCHERY-REARED JUVENILE CONCHS (*STROMBUS GIGAS* LINNÉ AND *S. COSTATUS* GMELIN)

RICHARD S. APPELDOORN AND ILSE M. SANDERS
Department of Marine Sciences
University of Puerto Rico
Mayagüez, Puerto Rico 00708

ABSTRACT The relationship between density and growth was examined for hatchery-reared juvenile conchs *Strombus gigas* Linné and *S. costatus* Gmelin. The individuals used were approximately 2 cm in length. Two experiments were conducted. Densities ranged from 120 to 720 • m^{-2} of tank bottom-surface area in the first experiment and 25 to 120 • m^{-2} in the second. Although the magnitude of growth, measured as the increase in siphonal length, varied between experiments, growth was consistently proportional to the inverse of density. No significant differences in growth were found between species.

KEY WORDS: growth, density, mariculture, *Strombus*, queen conch, milk conch

INTRODUCTION

Recent increased interest in the mariculture potential of the queen conch *Strombus gigas* Linné (see references in Berg 1981, Higman 1983) has paralleled the decline of conch fisheries throughout the Caribbean (Brownell and Stevely 1981). Although large-scale rearing of *Strombus* larvae is considered to be technically feasible (Ballantine and Appeldoorn 1983, Siddall 1983), many problems still need to be overcome for successful conch mariculture to become operational. One area requiring considerable research is growout. In particular, stocking density, especially with respect to growth, has been identified as an important factor in both intensive and extensive mariculture (Siddall 1984).

Growth of *Strombus gigas* can readily be observed in culture systems as a negative function of density. Laughlin and Weil (1983) recently presented quantitative data in this respect. They found that at lengths of less than 1 cm, growth at a density of 109 m^{-2} of tank area was 67% of that at 25 m^{-2}. As length increased, the effects of density on growth became more severe. Growth at 54 m^{-2} was only 40% of that at 17 m^{-2} for conchs 8.5 cm in length. On that basis, Laughlin and Weil (1983) recommended a density of 25 to 50 m^{-2} during the first year of laboratory culture. Siddall (1984) found increasing rates of movement and mucus production with stocking density and postulated these as possible factors influencing density-dependent growth. Woon (1983) using older juveniles, ranging from 13 to 27 cm in length and at a density of 25 m^{-2}, found only an increase in shell thickness, but not in length, over 45 days. Such shell thickening may be indicative of stress (Bryan 1969).

Field data on the relationship between density and growth were more equivocal. Iversen (1983) found no difference in growth for caged individuals (10 to 15 cm in length) at densities of 1 and 2 m^{-2}; however, caged individuals were characterized, in general, by poor growth. At lower densities (0.05 to 0.5 m^{-2}), a possible relationship was evident in the data of Alcolado (1976), but this relationship was confounded by temperature, which was inversely related to density.

In the present study the relationship between density and growth was investigated for *S. gigas* and the closely related milk conch *S. costatus* Gmelin. The purpose was to quantify this relationship at densities and sizes expected in a hatchery situation. Factors such as temperature or food type that would be expected to effect the magnitude of growth at any given density were not studied. The relative rate of change of growth at various densities was of interest, not the actual magnitude of growth.

MATERIALS AND METHODS

Growth experiments were conducted using laboratory-reared individuals of *S. gigas* and *S. costatus* (Ballantine and Appeldoorn 1983). A plexiglass experimental tank was built containing eight chambers (0.025 m^2 bottom area each) and receiving ambient seawater from a common settling chamber. Salinity was constant at 28 ppt. Flow rates for all chambers were similar at approximately 1.3 ℓ • min^{-1} yielding a turnover time of 2 min. Conchs were fed weekly with an excess of *Acanthophora spicifera* (Vahl), a macroalga known to elicit good growth in small juveniles (D. Ballantine, Dept. Marine Science, Univ. Puerto Rico, Mayagüez, PR; unpubl. data). Each week the chambers were cleaned, new food was added, and the conch groups were randomly repositioned. Growth was defined as the difference in siphonal length, the distance between the tip of the shell spire and the tip of the siphonal canal (the greatest shell dimension), measured at the beginning and end of the experiment. Lengths were measured to the nearest 0.1 mm using vernier calipers. If death occurred in any chamber, that individual was replaced by one of

similar size to maintain density. Subsequent analyses, however, only dealt with the original survivors.

Two 8-week experiments were conducted. The first began on 17 July 1983. For each species, groups of 3, 8, 13, and 19 individuals were randomly assigned chambers yielding densities of 120, 130, 520, and 720 m^{-2}, respectively. The mean size for each group was 22 mm for *S. gigas* and 20 mm for *S. costatus* (see Table 1). Daytime temperatures were very constant throughout the experiment averaging 29.8°C.

The second experiment began on 17 September. On the basis of the first experiment, the second employed lower densities. For each species, two groups of two and three individuals were randomly assigned chambers (80 and 120 m^{-2}, respectively). To investigate lower densities while maintaining the opportunity for interaction among individuals, two pairs of glass aquaria were used; the smaller aquaria were 731 cm^2; the larger were 1,213 cm^2. For each species three individuals were placed in each size tank resulting in densities of 25 and 41 m^{-2}, respectively. These were treated in the same manner as above. Conchs used for each species were taken from the groups of 19 individuals in the first experiment. Beginning lengths were approximately the same as before (see Table 1). Daytime water temperatures were similar to those of the first experiment (29°C) but nighttime temperatures, though not measured, were thought to be lower.

Linear regressions relating siphonal length to live weight were determined for both species. Thirty specimens of *S. gigas*, ranging from 26.5 to 37.0 mm, and 50 specimens of *S. costatus*, ranging from 21.1 to 58.5 mm, were measured as above for length. All conchs were then blotted to remove excess moisture, air dried, and weighed to the nearest 0.01 g.

RESULTS

Results of the two experiments are shown in Table 1. In the first, growth was greatly reduced at higher densities. The form of the relationship showed growth to be inversely proportional to density. A predictive regression of growth (in mm per 8-week experiment) versus the inverse of density (numbers m^{-2}) yielded the equation:

S. gigas Growth = $-1.08 + 1398$ (1/density)
$p < 0.01$, $r^2 = 0.785$

S. costatus Growth = $-0.39 + 1304$ (1/density)
$p < 0.05$, $r^2 = 0.835$

The second experiment resulted in a similar relationship, although absolute growth was lower and, with fewer numbers, results were more variable. Nevertheless, the results were significant:

S. gigas Growth = $-2.10 + 461$ (1/density)
$p < 0.01$, $r^2 = 0.912$

S. costatus Growth = $0.77 + 358$ (1/density)
$p < 0.05$, $r^2 = 0.806$

Although the regression lines for *S. costatus* had greater slopes within each experiment, the differences were not statistically significant, indicating a similar response between the two species. However, differences in the regression lines between experiments were statistically significant. The lower growth in the second experiment may indicate possible stunting, because these animals had shown no growth at high density during the first experiment. The regression lines are plotted in Figure 1. The following regressions can be used to convert siphonal length (mm) to biomass (g live weight):

S. gigas log (weight) = $3.992 + 2.871$ log (length)
$r^2 = 0.993$

S. costatus log (weight) = $-4.357 + 3.178$ log (length)
$r^2 = 0.980$

TABLE 1.

Mean initial length (mm) and growth increment (mm) observed per density (number m^{-2}) after 8 weeks.

Density	*Strombus gigas*			*Strombus costatus*		
	Initial Length (SD)	Growth	N[1]	Initial Length (SD)	Growth	N
			Experiment 1			
120	22.0 (1.16)	10.2 (0.85)	3	20.2 (1.15)	9.7 (1.85)	3
320	22.4 (2.67)	3.9 (1.04)	7[2]	20.1 (1.00)	4.8 (0.97)	8
520	22.8 (3.99)	1.7 (1.73)	13	20.1 (1.61)	2.1 (0.81)	13
720	22.7 (3.96)	0.5 (1.15)	19	20.5 (1.86)	0.6 (0.76)	19
			Experiment 2			
25	23.1 (2.33)	16.8 (0.35)	2[2]	21.3 (1.78)	16.6 (3.18)	2[2]
41	23.9 (2.88)	8.3 (0.94)	3	20.9 (1.51)	7.2 (0.20)	3
80	23.9 (1.26)	4.6 (2.27)	4	20.8 (0.95)	6.4 (1.70)	4
120	24.1 (2.49)	1.3 (1.63)	5[2]	20.0 (1.32)	3.7 (1.40)	6

[1] N = number of conchs measured.
[2] Sample size was reduced due to a single mortality during the experiment.

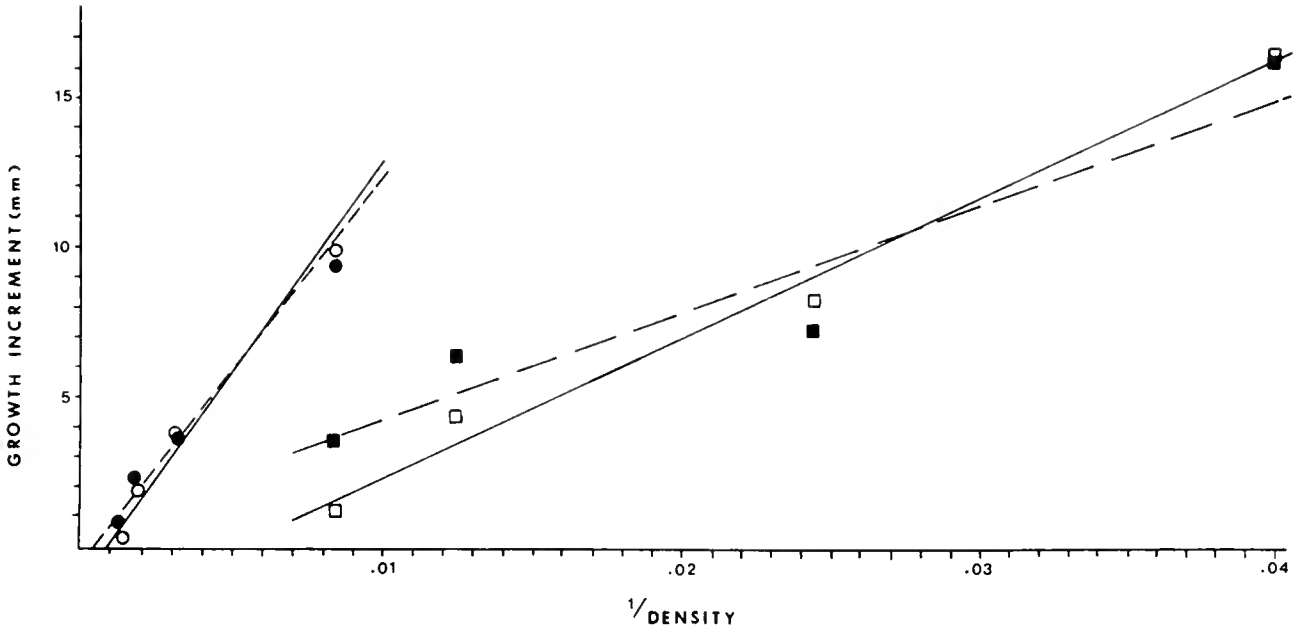


Figure 1. Growth increment over 8 weeks versus the inverse of density (number m^{-2}) for *Strombus gigas* (closed symbols) and *S costatus* (open symbols). Results for Experiments 1 and 2 are represented by circles and squares, respectively.

DISCUSSION

Current hatchery schemes, for both mariculture and fisheries management purposes, call for seeding juveniles in natural habitats (e.g., Ballantine and Appeldoorn 1983, Davis and Hesse 1983, Hensen 1983, Siddall 1983). In field-release studies, small laboratory-reared juveniles exhibited high mortality that appeared to be related to size (Appeldoorn and Ballantine 1983, Appeldoorn 1984). Based on these studies a large size-at-release (at least 50 to 60 mm) would be recommeded. This, however, means maintaining conchs for longer periods prior to release, or producing a considerable excess of individuals to compensate for mortality. In either case, the relationship between density and growth becomes important.

Results showed the relative reduction in growth increases with the inverse of density. Comparison of the two experiments indicated that the magnitude of growth will vary with conditions, such as prior growth history or temperature, but the inverse relationship with density remained. Moreover, in the second experiment using lower densities, growth decreased at an even greater relative rate than at the higher densities used in the first experiment. This result must be taken with some reservation, though, because conditions and resulting rates of growth differed between experiments. It does, however, reinforce the idea that growout time can be kept short only at reduced densities.

Factors other than density can affect the magnitude of growth. Therefore, growout densities should be determined with consideration for the conditions in which growth is maximum, or in which density effects are enhanced. One factor of importance is the known seasonality of growth (Alcolado 1976, Iversen 1983, Appledoorn, pers. observ.). Selected growout densities should be based on summer temperatures when both growth potential and density-dependent stresses (e.g., Siddall 1984) would be maximized.

There are several questions pertinent to density and growth that warrant further investigation. The mechanisms responsible for negative density-dependent growth remain undetermined. Siddall (1984) felt that increased movement and mucus production diverted energy away from growth. This is consistent with the observations of Creswell (cited by Siddall 1984) that at high density, although assimilation efficiency was unaffected, ingestion rates decreased indicating less time spent feeding, and food-conversion ratios increased indicating less biomass production and greater metabolic loss. How conchs assess density is also unclear. If density is determined by the encounter rate with other individuals or mucus trails, then density-dependent effects should increase to the square of length (i.e., surface area $\propto$ length^2). Siddall (1984) reported that conchs withdrew upon direct contact with the tissue of other conchs. On the other hand, if assessment of density is through detection of metabolites, then density-dependent effects should increase to the cube of length (i.e., weight $\propto$ length^3). It is evident by the rapid onset of their escape response in the presence of predators (Robertson 1961, Appeldoorn and Ballantine 1983) that conchs have sensitive chemoreception and can detect other organisms at a distance. The resolution of these questions should provide basic information necessary for the intelligent design of growout procedures and facilities.

ACKNOWLEDGMENTS

The authors thank D. L. Ballantine, S. E. Siddall, and R. Mann for critically reviewing the manuscript. This work was funded by the U.S. National Marine Fisheries Service (Contract No. NA81–GA–C–0015).

REFERENCES CITED

Alcolado, P. M. 1976. Growth, morphological variations of the shell and some biological data of the conch *Strombus gigas* L. (Mollusca, Mesogastropoda). *Acad. Cienc. Cuba Ser. Oceanol.* 34:26 p. (English translation)

Appeldoorn, R. S. 1984. The effect of size on mortality of small juvenile conchs (*Strombus gigas* Linné and *S. costatus* Gmelin). *J. Shellfish Res.* 4(1):37–43.

_____ & D. L. Ballantine. 1983. Field release of cultured queen conchs in Puerto Rico: Implications for stock restoration. *Proc. Gulf Caribb. Fish. Inst.* 35:89–98.

Ballantine, D. L. & R. S. Appeldoorn. 1983. Queen conch culture and future prospects in Puerto Rico. *Proc. Gulf Caribb. Fish. Inst.* 35:57–63.

Berg, C. J., Jr., editor. 1981. *Proceedings, Queen Conch Fisheries and Mariculture Meeting.* January 1981. Freeport, The Bahamas: Wallace Groves Aquaculture Foundation. 46 p.

Brownell, W. N. & J. M. Stevely. 1981. The biology, fisheries and management of the queen conch, *Strombus gigas. U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 43(7):1–12.

Bryan, G. W. 1969. The effects of oil-spill removers ("detergents") on the gastropod *Nucella lapillus* on a rocky shore and in the laboratory. *J. Mar. Biol. Assoc. U.K.* 49:1067–1092.

Davis, M. & C. Hesse. 1983. Third world level conch mariculture in the Turks and Caicos Islands. *Proc. Gulf Caribb. Fish. Inst.* 35:73–82.

Hensen, R. R. 1983. Queen conch management and culture in the Netherlands Antilles. *Proc. Gulf Caribb. Fish. Inst.* 35:53–56.

Higman, J. B., editor. 1983. *Proceedings of the Thirty-fifth Annual Gulf and Caribbean Fisheries Institute.* Miami, FL. 208 p.

Iversen, E. S. 1983. Feasibility of increasing Bahamian conch production by mariculture. *Proc. Gulf Caribb. Fish. Inst.* 35:83–88.

Laughlin, R. A. & E. Weil M. 1983. Queen conch mariculture and restoration in the Archipielago de Los Roques. *Proc. Gulf Caribb. Fish. Inst.* 35:64–72.

Robertson, R. 1961. The feeding of *Strombus* and related herbivorous marine gastropods: With a review and field observations. *Not. Nat. (Phila.)* 343:9 p.

Siddall, S. E. 1983. Biological and economic outlook for hatchery production of juvenile queen conch. *Proc. Gulf Caribb. Fish. Inst.* 35:46–52.

_____. 1984. Density-dependent levels of activity of juveniles of the queen conch *Strombus gigas* Linné. *J. Shellfish Res.* 4(1):67–74.

Woon, G. L. 1983. Preliminary algal preference studies and observations of conchs, *Strombus gigas* Linné and *Strombus costatus* Gmelin, held in high density. *J. World Maricul. Soc.* 14:162–163.

Journal of Shellfish Research, Vol. 4, No. 1, 67–74, 1984.

DENSITY–DEPENDENT LEVELS OF ACTIVITY OF JUVENILES OF THE QUEEN CONCH *STROMBUS GIGAS* LINNÉ

SCOTT E. SIDDALL
Marine Sciences Research Center
State University of New York
Stony Brook, New York 11794

ABSTRACT Juveniles of the queen conch *Strombus gigas* Linné grow slowly at high-population densities in the laboratory and in the field, even when food resources appear to be unlimited. One possible explanation for this phenomenon is that juvenile conchs expend less energy growing and more energy interacting with each other at high-population densities. A series of experiments was conducted to evaluate the consequences of interactions among juveniles. Five-month-old queen conch juveniles (mean siphonal length, 0.95 cm) were held at population densities of 0.05, 0.25, and 0.50 cm^{-2} of available space. Examination of time-lapse photographic records showed that juveniles are capable of traveling an average of 36.1 cm^{-1} • hr which equals 38 body lengths • hr^{-1}. Juveniles held at 0.50 cm^{-2} moved significantly more than those held at 0.05 or 0.25 cm^{-2}. Mucus produced by conchs during travel was collected, dried, and weighed at the end of each experiment. More mucus was recovered per juvenile (142.7 μg dry weight • $conch^{-1}$ • hr^{-1}, or approximately 2.9% of dry tissue weight • hr^{-1}) at high-population densities than at low densities. Increased locomotory activity and mucus production occurring at high densities at least partially explain declining growth rates in spite of unlimited food resources.

KEY WORDS: Queen conch, *Strombus gigas*, population density, locomotion, mucus secretion

INTRODUCTION

Recent laboratory and field studies have shown that growth rates of juveniles of the queen conch *Strombus gigas* Linné are significantly reduced when the animals aggregate in high densities (Laughlin and Weil 1983, Appeldoorn and Sanders 1984, Creswell 1984, Weil and Laughlin 1984). These negative effects of crowding on growth rates are important for three reasons.

(1) Queen conch juveniles and adults tend to aggregate naturally. Dense assemblages of juveniles may result from the patchy nature of larval recruitment; however, as the population matures, dense groups of a single size-range (presumably the same age-class) often remain aggregated, gradually moving offshore as adults (Randall 1964, Hesse 1976, 1979). Sustained densities as high as 5 juveniles (8 to 10 cm siphonal length = tip of siphonal canal to apex of shell = maximum shell length) per m^2 or 1 adult (22 to 24 cm) per m^2 have been observed by the author in hectare-size plots in the Bahamas. Highest mean densities for areas surrounding the Berry Islands, Bahamas, were 1.96 juveniles • m^{-2} according to unpublished analyses by E. Rutherford and E. Iversen (Univ. Miami, Miami, FL; pers. comm.). Large juveniles are known to assemble in extremely dense clumps (3 to 10 conchs deep) during winter months (Hesse 1979; Hesse, Foundation for PRIDE, Miami, FL; pers. comm.). Tag and recapture studies have demonstrated that growth rates of individuals within naturally occurring high-density groups are significantly lower than those of isolated individuals or less-dense populations (Weil and Laughlin 1984).

(2) The queen conch is an important living marine resource. Throughout the Caribbean, Bahamas, and northern coasts of South America, landings of the queen conch are second in value only to the spiny lobster (Brownell and Stevely 1981). The species is heavily overfished in a variable, but often profitable, commercial fishery that competes with critical subsistence needs of many lesser developed island nations.

(3) High-density culture of juveniles is an obligatory and major step in the production of juveniles for natural-stock replenishment or growout to market size. Mariculture production of juveniles of the queen conch has been demonstrated (Brownell 1977, Ballantine and Appeldoorn 1983, Davis and Hesse 1983, Siddall 1983), and a number of international public and private enterprises have stated objectives of supplying juveniles (seed) for establishing self-sustaining populations, for reestablishing and maintaining overfished stocks, or for vertically integrated production and marketing of a conch product (Siddall 1984).

It is not new or surprising that growth rates depend upon population density; the relationship has been described for many invertebrates, including other prosobranchs (Anderson 1971, Fenchel and Kofoed 1976). In general, the relationship has been attributed to spatial interactions which alter the feeding opportunity or behavior of the snail or affect other nonfeeding activities of the animal such as locomotion, mucus production, maintenance of territoriality or emigration efforts (Levinton 1979).

For *Strombus* specifically, food-related effects might include intraspecies competition for limited food types and quantities, grazing rates that exceed renewal rates of the food resource, or individual interactions that result in lower ingestion rates. It is clear from field studies of captive populations (Iversen 1983) that the food resource (epiphytic microalgae, fleshy macroalgae, and detritus; see Berg 1974) is scarce and easily overgrazed.

Distinct territorial behavior is unknown for the queen conch, and the natural occurrence of slow growing, dense populations of juveniles suggests that the species does not necessarily react to overcrowding by emigration. Locomotion, on the other hand, is so slow as to be very difficult to observe over periods of less than one hour. Queen conchs frequently move by a thrusting motion ("leaping"), but can also glide across surfaces leaving a mucus trail (Parker 1922; Randall 1964; Berg 1974, 1975). Mucus production is partly a function of the distance traveled.

The nature of the density-dependent, growth-rate relationship for queen conchs has been more fully characterized in recent studies. Creswell (1984) showed that ingestion rates and growth declined as experimental-stocking densities increased. Queen conch juveniles (5 to 25 mm siphonal length) ingested significantly less *Enteromorpha* sp. as food when held at 0.06 juvenile · cm^{-2} than when held at 0.01 juvenile · cm^{-2}. In Creswell's study, *Enteromorpha* was ranked as one of the best diets tested and for the study of ingestion rates, *Enteromorpha* was always provided in excess. Although there was no effect of density on assimilation efficiency, over a 21-day period conch juveniles gained nearly 25% of their initial wet-tissue weight at low-stocking density, yet gained only 8.2% at high-stocking density. Similarly, food-conversion ratios were significantly higher at high-stocking densities than at low-stocking densities (significant at the 99% confidence level). Additionally, in laboratory experiments lasting 6 weeks, Appeldoorn and Sanders (1984) showed that growth of juveniles of *S. gigas* and *S. costatus* Gmelin declined consistently with increasing population density over the range of 0.003 to 0.072 juvenile · cm^{-2}. Clearly, population density affects the feeding relationships of queen conch juveniles in the laboratory.

Laughlin and Weil (1983) and Weil and Laughlin (1984) conducted tag-and-recapture studies of field populations of conchs in areas surrounding the Dos Mosquises Marine Station, Venezuela, where natural foods were present in apparent excess and conch growth rates were high (>0.9 cm · mo^{-1}). They found a significant reduction in growth of juveniles (< 5 cm) at population densities greater than 0.01 · cm^{-2} and that effects on growth became more pronounced as the conchs grew.

None of these studies specifically examined the effects of population density on nonfeeding activities, such as locomotion and mucus production. Although it is likely that feeding of juvenile conchs in dense aggregations may be limited by competition and overgrazing, it is also possible that nonfeeding activities associated with behavioral interactions represent significant energy losses, especially during the warm summer growth season when the snails are most active (Hesse 1976).

Strombid snails are capable of complex behaviors (Berg 1975, Perchade 1982, Bradshaw-Hawkins and Sander 1983) and have relatively well-developed sensory abilities. The *Strombus* eye is complex, can detect movement and shadows, is capable of regeneration, and is one of the more advanced visual organs in the invertebrates (Figure 1; Hughes 1976, Gillary 1977). Some evidence suggests that *Strombus* has the chemosensory ability to detect predatory gastropods (Berg 1974, Field 1977).

A series of experiments was conducted to evaluate the consequences of interactions among juvenile queen conchs. The specific objectives were (1) to examine the relationship between rate of movement and population density, and (2) to estimate rates of mucus production as a function of distance traveled and population density.

MATERIALS AND METHODS

Several hundred juveniles of *S. gigas* were selected from a hatchery-produced population of approximately 3,000. Juveniles were reared under conditions outlined elsewhere (Siddall 1983) from three naturally produced egg masses collected from Biscayne Bay, Florida. Juveniles used in these experiments (mean siphonal length, 0.95 ± 0.11 cm; range, 0.72 – 1.17 cm) were 5 months old (after hatching). Prior to the experiments conducted in April 1983, all juveniles were maintained in outdoor raceways of flowing seawater at 26 to 29°C while being fed a mixed, natural diet consisting mainly of *Ceramium* sp., *Enteromorpha* sp., and *Spyridia filamentosa* (Wulfen). Compared to other studies of natural populations of juveniles (Iversen 1983), the mean growth rate of the experimental population was high (0.40 cm · mo^{-1} during the month preceeding the experiments) and the animals were normally active. Juveniles were used only once in the experiments after which they were maintained separately for growout and observation.

Data collection involved time-lapse photographic records of the movement of the juveniles held at different population densities. After each experiment, mucus produced during the movement of the juveniles was collected and weighed.

For each experiment, juvenile conchs were held at densities of 0.05, 0.25, and 0.50 individual · cm^{-2} in clean, glass culture dishes (16 cm in diameter) which were filled to a depth of 5 cm with 5-μm filtered seawater. No potential food items were provided during the experiments. Because at no time did the juveniles climb the vertical surfaces of the dishes, only the bottom-surface area of 201 cm^2 was used to establish population densities. Only two population densities (0.05 and 0.50 or 0.25 and 0.50 · cm^{-2}) were filmed at a time (Figure 2A).

Prior work suggested that light levels might affect the behavior of the juveniles. Flash photography clearly retarded movement of the juveniles. Thus, all experiments were conducted outdoors in indirect sunlight on clear days. Variations in seawater temperature during the experiments were slight (26.8 – 27.9°C). All experiments were begun between 1000 and 1200 hours local time (Miami, FL). Juveniles were allowed to acclimate to the experimental

conditions for one hour after which time a clock was placed in the photographic field (see Figure 2A) and an 8-mm-motion picture camera equipped with an intervalometer was started. Exposures of both dishes and the clock were made every 7 seconds for 6.3 hours (completing a standard 3-minute film cartridge).

At the end of the filming period, all juveniles were carefully removed from each dish. In an effort to minimize dissolution of the mucus trails adhering to the glass dishes, cetylpridimium chloride (Sigma Chemical Co., C9002®) was added to the seawater (10 g · l^{-1}) remaining in the dishes (see Oster and Pollister 1955). After 30 minutes, the seawater was drained from both dishes in each experiment and the mucus carefully removed by scraping with flat dissecting razors. Compared to untreated samples of mucus, the cetylpyridimium chloride treatment "hardened" the mucus strands and made them considerably easier to handle. Evans blue (dissolved in seawater) was used to stain and disclose any remaining mucus which was subsequently collected (Figure 2B). Mucus gathered in this manner was rinsed in distilled water for no more than 2 to 3 seconds then dried at 40°C for 1 hour on aluminum foil sheets. Dried mucus was weighed to the nearest 1.0 μg on a Cahn Electrobalance (model 26). Opportunities to conduct experiments on mucus production were limited; therefore, I was unable to validate these procedures for recovering mucus or to calculate error rates. After acclimating, the conchs could not be disturbed to remove mucus secreted during the one hour of acclimation. Rate calculations are based on the total 6.3-hour experimental period and, therefore, average out any possible differences in rates of secretion between periods of acclimation and filming. Estimated rates of mucus production per juvenile per hour were calculated as:

total dw of mucus recovered/number of juveniles at that density/7.3 hrs (1 hr acclimation + 6.3 hrs filming)

where dw = dry weight. In this manner six measurements of mucus produced were made (three at a low-population density of 0.05 juvenile · cm^{-2} and three at a high-population density of 0.50 juvenile · cm^{-2}).

After processing, the film records were slowly projected on a gridded chalkboard so that the path of each individual could be traced over the 6.3 hours of each experiment. The clock included in the image provided an accurate time reference. Actual distances traveled per hour were determined by measuring the chalkboard tracings for each juvenile and

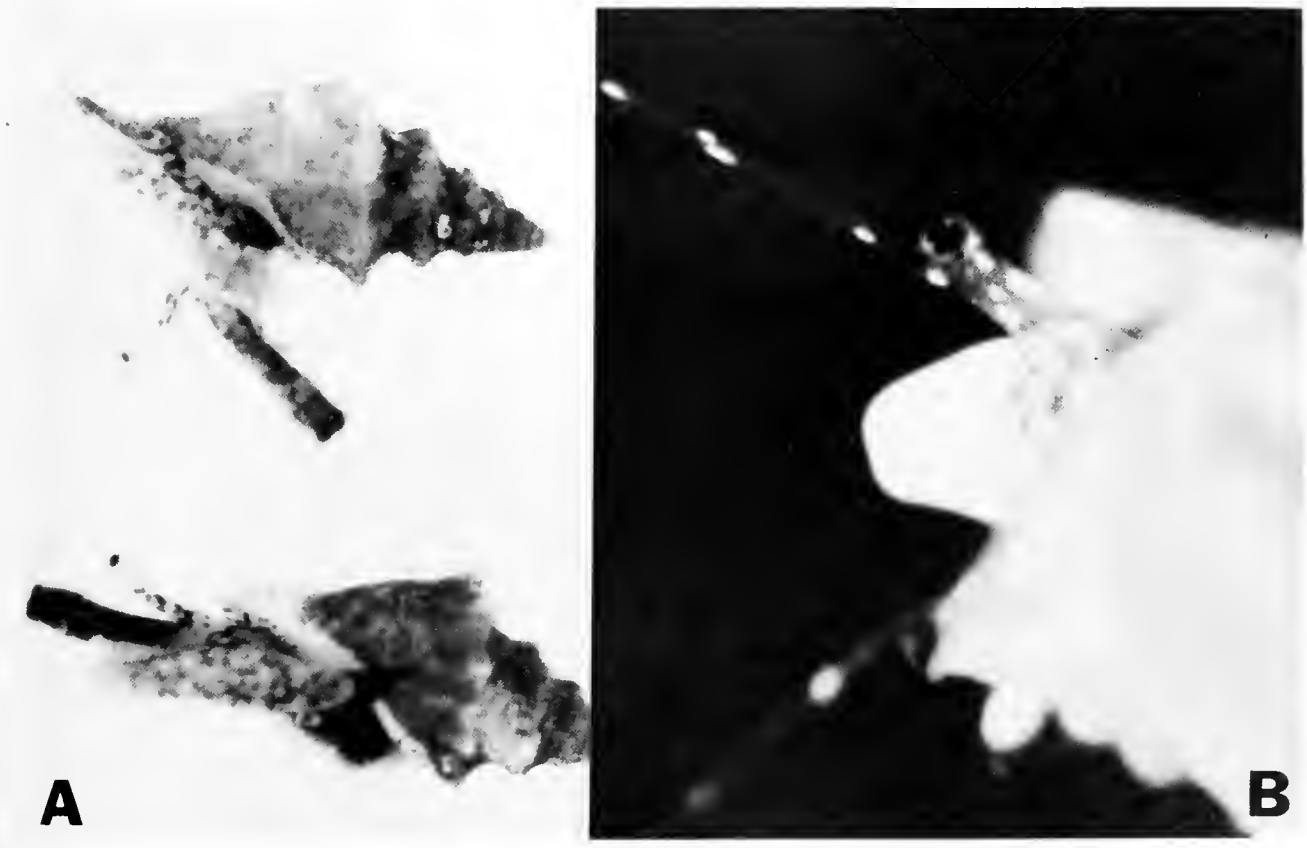


Figure 1. (A) Five-month-old juveniles of the queen conch *Strombus gigas* Linné (siphonal length = 1.1 cm) viewed through a glass on which they are gliding. Probosces and eyestalks are frequently directed toward other queen conch juveniles. (B) Developing eyestalk of a juvenile queen conch, one week after metamorphosis (siphonal length = 0.25 cm).

converting the tracings to cm by calibrating them with the projected image of the dishes known to be 16 cm in diameter. Fifty observations of distance traveled were made for each of three population densities (0.05, 0.25, and 0.50 juvenile $\cdot$ cm^{-2}). One-way analyses of variance (effect of density on distance traveled and on mucus recovered) and Student-Newman-Keuls multiple range tests ($a = 0.05$) were conducted with subprograms of SPSS (Nie et al. 1975).

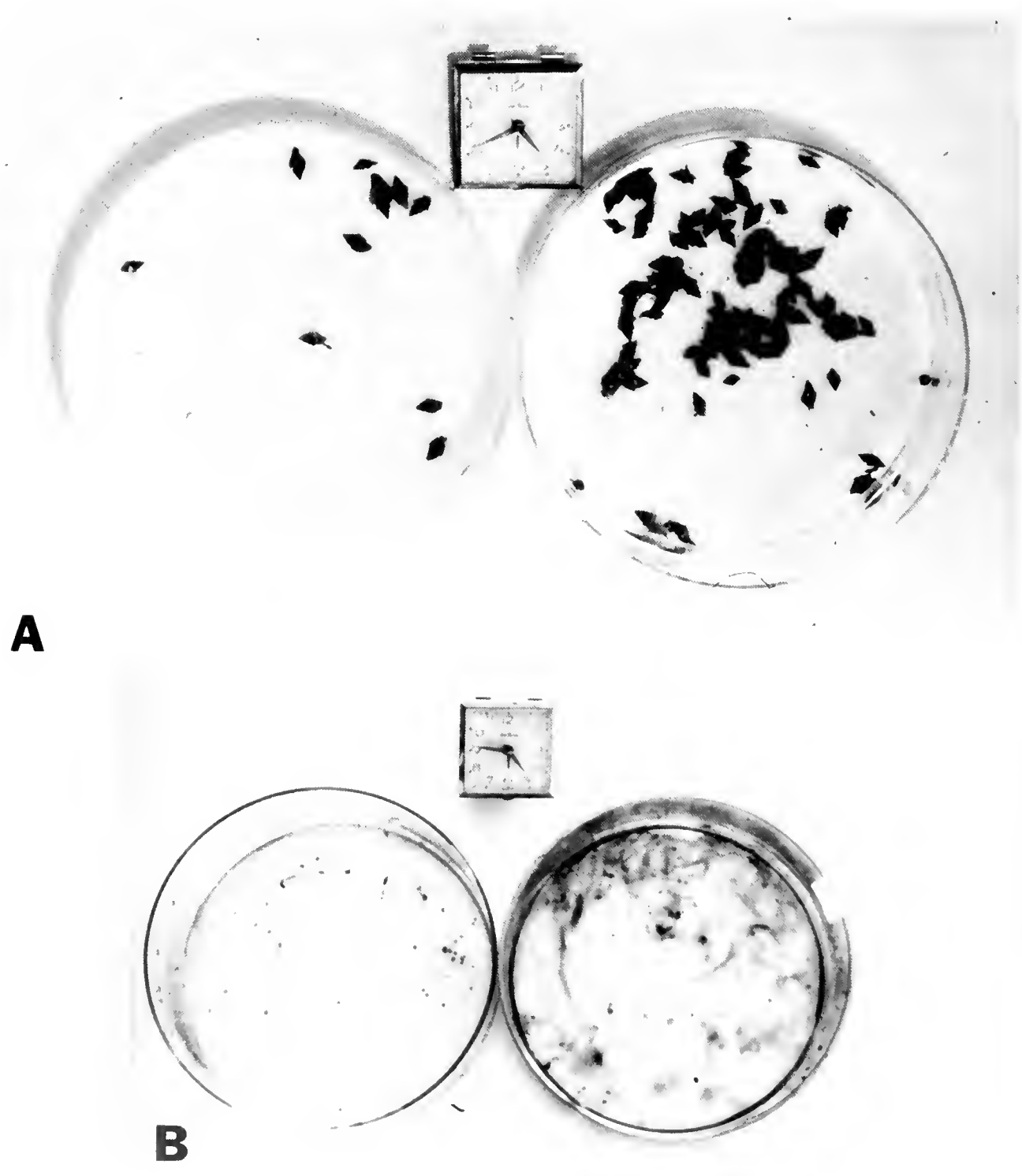


Figure 2. (A) Field of view of experiments as filmed by time-lapse photography. The left dish holds 10 juvenile queen conchs (0.05 $\cdot$ cm^{-2}); the right dish holds 100 (0.50 $\cdot$ cm^{-2}). Clock included in motion picture images for time reference and speed calculations. (B) Same field of view as (A) after juveniles were removed and mucus trails were stabilized and stained.

RESULTS

Table 1 summarizes the analysis of experimental effects of population density on distance traveled. At the highest density of 0.50 juvenile · cm^{-2}, the conchs moved an average of 36.1 cm · hr^{-1} which was significantly more ($p \leq 0.01$) than their movement at either of the lower densities.

TABLE 1.

Effect of population density on distance traveled (Student-Newman-Keuls multiple range test; a = 0.05).

conchs/cm^2	0.05	0.25	0.50
Mean distance traveled cm/hr	21.3	26.0	36.1
Number of individual observations	50	50	50

For purposes of comparison, laboratory and field estimates of rates of movement for other mesogastropods are summarized in Table 2.

Rates of movement may be expressed in units of body length (siphonal length). At the lower population densities tested in the present study, juveniles moved 22 to 27 shell lengths · hr^{-1}, while at the higher density, they moved 38 shell lengths · hr^{-1}. These estimates are much higher than those calculated from Hazlett's (1984) field data for *Cerithium litteratum* (Born) (1.3 shell lengths · hr^{-1}), but they correspond reasonably well with rates of movement of larger juveniles of *Strombus gallus* Linné (16.4 shell lengths · hr^{-1}) and of *Xenophora conchyliophora* (Born) (26.6 shell lengths · hr^{-1}) calculated from Berg's (1975) data. Although Berg's estimates were made from field observations over a 24-hr period, he expressed rates in terms of length · min^{-1}. I have recalculated those rates in units of length · hr^{-1}, but this may not necessarily mean that such rates were sustained over hour-long intervals.

Hazlett (1984) indicated that disturbance (relocation for experiments) did not significantly influence the movements of most of the snails in his field study. To examine this possibility in my laboratory studies, the 6.3-hr experimental period (following 1 hr of acclimation) was arbitrarily broken down into three 2.1-hr intervals and mean rates of movement were calculated for each interval. There were no significant differences in mean distances traveled · hr^{-1} among the intervals within any of the density treatments ($p = 0.263$ at 0.05 conch · cm^{-2}; $p = 0.144$ at 0.25 conch · cm^{-2}; $p = 0.389$ at 0.50 conch · cm^{-2}). Therefore, after the period of acclimation, no effects of disturbance from setting up the experiments were detected.

Although the direction of each juvenile's movements may not have been random, the tracings rarely revealed any sustained, unidirectional movement. Intertidal gastropods do not sustain movement in a straight line (Hamilton 1978, Hazlett 1984). Juveniles at all densities tended to wander around the dish perimeter as well as across the dish. At all densities, the conchs withdrew from direct contact with other conchs except when only the shell contacted other shell material and no tactile tissue was involved. No mucus was observed on the shells of other juveniles.

Table 3 presents the analysis of estimated rates of mucus production on a per capita basis. Juveniles held at high-population densities produced nearly three times as much mucus per conch per hour as did the low-density populations.

The dry weight of mucus recovered per conch can be expressed as a proportion of the conch's dry-tissue weight using relationships from Creswell's (1984) study. The mean siphonal length of the juveniles in this study, 0.95 cm, corresponds to a 49.8-mg whole wet weight, a 39.1-mg wet-tissue weight, and a 5.01-mg dry-tissue weight. Hence, the high-density population was secreting a mean of 2.9% (0.1427 mg · 5.01 mg^{-1}) of their dry-tissue weight per hour,

TABLE 2.

Reported rates of movement for other mesogastropods.

Species	Size (cm)	Distance Traveled (cm · hr^{-1})	Study Site	Reference
Cerithium litteratum (Born)	1.70 – 1.75	2.2	Field	Hazlett 1984
C. litteratum	n/a	0.1	Laboratory	Linsley 1978
C. guinaicum Philippi	n/a	0.3	Laboratory	Linsley 1978
C. nodulosum Bruguière	n/a	0.7	Field	Hazlett 1984
Littorina irrorata (Say)	1.85	20–25 (cm per activity period, 12 hr?)	Field	Hamilton 1978
L. littorea (Linné)	n/a	130	Field	Gowantoch and Hayes 1926
Strombus gallus Linné	9.2*	151.2	Field	Berg 1975
Xenophora conchyliophora (Born)	3.25*	86.4	Field	Berg 1975

*Calculated from tabulated data of movement and expressed as a percentage of shell length.

TABLE 3.

Effect of population density on quantity of mucus recovered (Student-Newman-Keuls multiple range test; a = 0.05).

Conchs/cm^2	0.05	0.50
Mean dry weight of mucus (μg • conch^{-1} • hr^{-1})	59.7	142.7
Conch tissue weight • hr^{-1} (%)	1.2	2.9
Number of observations	3	3
Number of conchs/observation	10	100

almost 2.5 times as much as their low-density counterparts. Finally, if the mean-distance traveled is divided by the mean dry weight of mucus recovered, the amount of mucus secreted per cm traveled can be estimated. At low density, 2.8 μg dry-weight mucus were recovered for each cm traveled. At high density, 3.9 μg • cm^{-1} were recovered.

DISCUSSION

It is clear from these experiments that there is a direct relationship between rates of movement and population density. This relationship may represent a behavioral adaptation only to severe overcrowding, in which case, it may be an extreme reaction to artifically high population densities. Therefore, it is important to consider the artificial nature of the experimental setting when interpreting these results because they may not reflect natural relationships in the field.

It is likely that the experimental densities were unnaturally high. There are no data on natural densities for comparison with the experimental densities used here because juveniles less than 5 cm siphonal length have been found only rarely in field studies (Randall 1964, Davis and Hesse 1983). Furthermore, small juveniles may bury themselves as deep as 15 cm in sandy substrates (E. Iversen, Univ. Miami, Miami, FL; unpubl. data) and thereby distribute themselves in three dimensions rather than over a surface area of two dimensions. Population densities for buried juveniles must be calculated on the basis of cubic units (cm^3). Older juveniles, adults, and the experimental conchs in this study did not or could not bury, therefore, the population densities must be calculated in terms of square units (cm^2).

The experimental environment was unlike the natural habitat. The clean, glass dishes did not contain any sand or coral rubble substrate, nor were there any objects (e.g., *Thalassia* sp. fronds or rhizomes) which might mediate behavioral interactions in field populations. Juveniles may orient themselves with respect to patterns of seawater flow yet there were no currents in these static experiments. Water quality did not appear to vary significantly; dissolved oxygen was measured at the end of two of the high-density experiments (YSI Model 51 oxygen meter) at 85 and 91% saturation (26°C and 33 ppt).

It is appropriate, however, to interpret these experiments in view of mariculture production, specifically the intermediate or "nursery" growout phase from metamorphosis to reseeding (transplantation) size. The nursery habitat is more like the laboratory setting of Creswell (1984) or this study than the natural habitat. Production of juveniles must be cost effective; therefore, the nursery system must operate at high densities and must produce sufficiently large juveniles (> 1.0 cm according to unpublished results of L. FitzGerald [Univ. Miami, Miami, FL] in the Florida Keys; possibly larger than 2.5 cm according to Siddall [1983]; or even larger according to Appeldoorn and Ballantine [1983] or Jory and Iversen [1983]).

The trends reported here and by Creswell (1984) and by Weil and Laughlin (1984) compare with those obtained for *Hydrobia ventrosa* (Montagu), a much smaller prosobranch (Anderson 1971, Fenchel and Kofoed 1976, Levinton 1979) in that ingestion rates and growth rates declined at high densities. Unlike *Hydrobia*, for which Levinton (1979) described a significant depression of activity with increasing density, *Strombus gigas* became more active in these high-density laboratory settings. Although many complexities of the natural habitat might modify this relationship in the field, it is clear that lowered ingestion rates and elevated levels of activity would adversely affect captive populations of juveniles in a mariculture growout system. Thus, nursery-growout facilities for queen conchs should be designed to minimize interactions among the juveniles either through provision of adequate space in three dimensions (likely to an expensive solution) or of barriers that would reduce contact among juveniles.

Linsley (1978) presumed there would be a correlation between the size of a strombid snail and its potential rate of locomotion primarily because the length of "stride" would be important for a gastropod that leaps (Berg 1975). Conversely, Linsley discussed the lack of a clear relationship between size of snails that glide and rates of movement. Although the queen conch is capable of leaping behavior even as a competent veliger (Siddall, pers. observ.), the artificial setting of these experiments or in an experimental nursery (Siddall 1983) or in other studies of captive conchs (Hesse 1979), juveniles emphasized the gliding mode of locomotion. This is especially true for small juveniles that can carry their own weight as they glide up vertical surfaces in search of food (see Figure 3). Therefore, in these situations, rates of movement are not likely to be strongly related to size. More importantly, in situations where juveniles choose to glide more than leap, the production of mucus apparently becomes a potentially significant investment of energy.

Results from the mucus-production experiments must be interpreted with caution because there are too few replicates to establish the reproducibility of these data. The difference between the two groups of three measurements

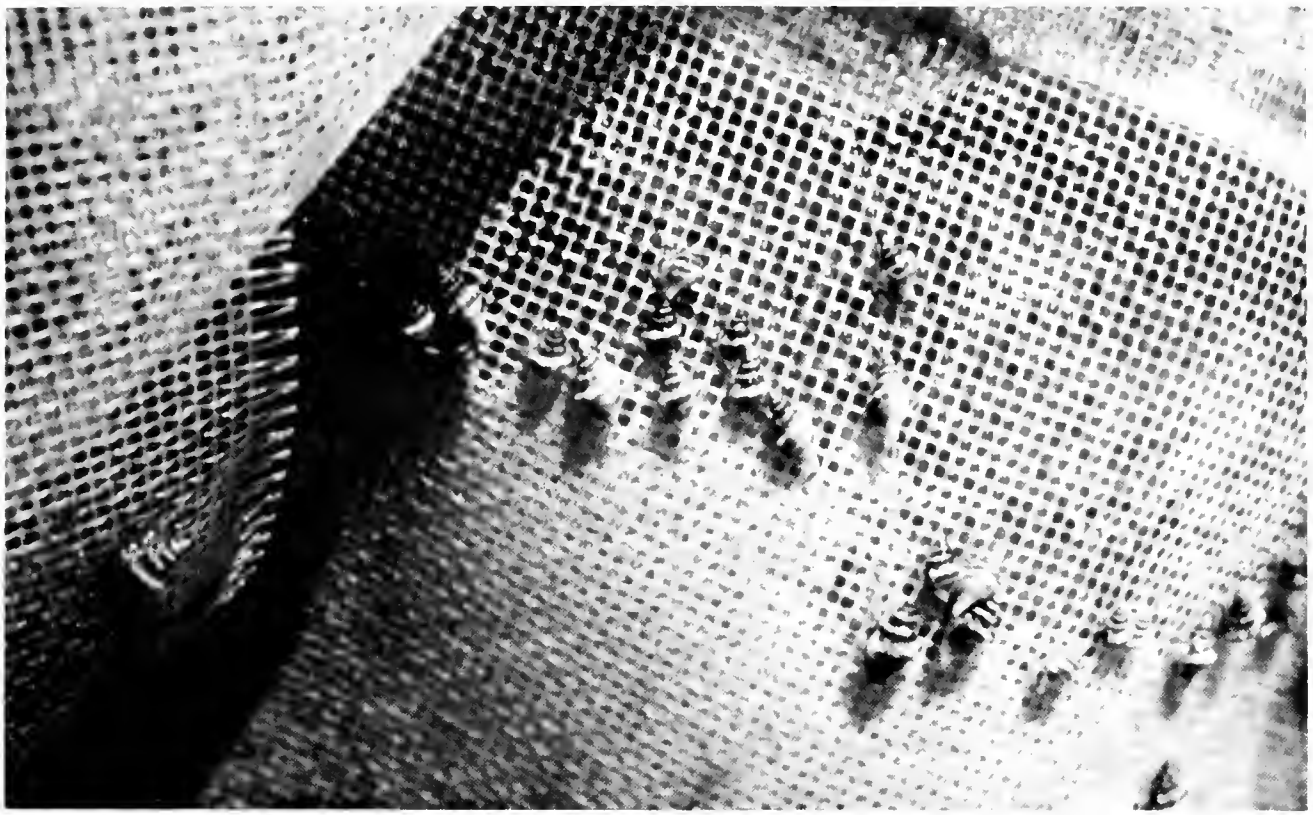


Figure 3. High-density aggregation of juveniles of the queen conch *Strombus gigas* (0.8 to 1.4 cm) grazing on epiphytic algae on plastic screen in an experimental nursery raceway.

was significant at the 95% confidence level; however, the calculated rate of mucus production under high-density conditions (2.9% dry-tissue weight · hr^{-1}) seems to be unrealistically high. Kofoed (1975) estimated that secretion of mucus constituted approximately 9% of the carbon assimilated by the deposit-feeding prosobranch *Hydrobia ventrosa*. If queen conch juveniles were capable of sustaining the rates of secretion estimated in the present study, feeding activities would have to compensate for a 34.8% loss of body weight every 12 hr. It has not been shown that the relatively high rates of ingestion of which the queen conch juveniles are capable (Creswell 1984) could compensate for such losses.

These procedures for estimating mucus production are useful in a relative sense; thus, comparisons between these low- and high-population density experiments are possible. Secretion of mucus significantly increased at high-population densities probably because distances traveled increased at high densities; however, rates of mucus production per cm traveled also increased significantly at high-population densities. This suggests that mucus production is not a simple function of distance traveled but rather a more complex density-dependent response.

REFERENCES CITED

Anderson, A. 1971. Intertidal activity, breeding and the floating habit of *Hydrobia ulvae* in the Ythan estuary. *J. Mar. Biol. Assoc. U.K.* 51:423–437.

Appeldoorn, R. S. & D. L. Ballantine. 1983. Field release of cultured queen conch in Puerto Rico: Implications for stock restoration. *Proc. Gulf Caribb. Fish. Inst.* 35:89–98.

Appeldoorn, R. S. & I. M. Sanders. 1984. Quantification of the density-growth relationship in hatchery-reared juveniles of *Strombus gigas* Linné and *S. costatus* Gmelin *J. Shellfish Res.* 4(1):63–66.

Ballantine, D. L. & R. S. Appeldoorn. 1983. Queen conch culture and future prospects in Puerto Rico. *Proc. Gulf Caribb. Fish. Inst.* 35:57–72.

Berg, C. J., Jr. 1974. A comparative ethological study of strombid gastropods. *Behaviour* 51:274–322.

_____ . 1975. Behavior and ecology of conch (Superfamily Strombacea) on a deep subtidal algal plain. *Bull. Mar. Sci.* 25(3): 307–317.

Bradshaw-Hawkins, V. I. & F. Sander. 1983. Notes on the reproductive biology and behavior of the West Indian fighting conch, *Strombus pugilis* Linnaeus in Barbados, with evidence of male guarding. *Veliger* 24(2):159–164.

Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas, S. costatus* and *S. pugilis* in Los Roques, Venezuela. *Bull. Mar. Sci.* 27:668–680.

_____ & J. M. Stevely 1981. The biology, fisheries, and management of the queen conch, *Strombus gigas*. *U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 43(7):1–12.

Creswell, R. L. 1984. Ingestion, assimilation and growth of juvenile queen conchs, *Strombus gigas*, fed experimental diets. Miami, FL: Univ. of Miami, Rosenstiel School of Marine and Atmopsheric Science. 108 p. Thesis.

Davis, M. & C. Hesse. 1983. Third world level conch mariculture in the Turks and Caicos Islands. *Proc. Gulf Caribb. Fish. Inst.* 35:73–82.

Fenchel, T. & L. H. Kofoed. 1976. Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos* 27: 367–376.

Field, L. H. 1977. An experimental analysis of the escape response of the gastropod *Strombus maculatus*. *Pac. Sci.* 31:1–11.

Gillary, H. L. 1977. Electrical potentials from the eye and optic nerve of *Strombus:* Effects of electrical stimulation of the optic nerve. *J. Exp. Biol.* 66:159–171.

Gowanloch, J. N. & F. R. Hayes. 1926. Contributions to the study of marine gastropods. I. The physical factors, behaviour and intertidal life of *Littorina*. *Contrib. Can. Biol. Fish. N.S.* 3: 133–165.

Hamilton, P. V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Mar. Biol. (Berl.)* 46:49–58.

Hazlett, B. A. 1984. Daily movements of some tropical marine gastropods. *Mar. Behav. Physiol.* 10:1–14.

Hesse, K. O. 1976. An ecological study of the queen conch, *Strombus gigas*. Storrs, CT: Univ. of Connecticut. 107 p. Thesis.

_____ . 1979. Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. *Bull. Mar. Sci.* 29(3):303–311.

Hughes, H. P. I. 1976. Structure and regeneration of the eyes of strombid gastropods. *Cell Tissue Res.* 171:259–271.

Iversen, E. S. 1983. Feasibility of increasing Bahamian conch production by mariculture. *Proc. Gulf Caribb. Fish. Inst.* 35:83–88.

Jory, D. E. & E. S. Iversen. 1983. Queen conch predators: not a roadblock to mariculture. *Proc. Gulf Caribb. Fish. Inst.* 35: 108–111.

Kofoed, L. H. 1975. The feeding biology of *Hydrobia ventrosa* (Montagu). II. Allocation of the components of the carbon-budget and the significance of the secretion of dissolved organic material. *J. Exp. Mar. Biol. Ecol.* 19:243–256.

Laughlin, R. A. & E. Weil M. 1983. Queen conch mariculture and restoration in the Archipielago de los Roques: Preliminary results. *Proc. Gulf Caribb. Fish. Inst.* 35:64–72.

Levinton, J. S. 1979. The effect of density upon deposit-feeding populations: Movement, feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). *Oecologia (Berl.)* 43:27–39.

Linsley, R. M. 1978. Locomotion rates and shell form in the Gastropoda. *Malacologia* 17(2):193–206.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner & D. H. Bent. 1975. *Statistical Package for the Social Sciences: SPSS.* 2nd ed. New York, NY:McGraw-Hill. 675 p.

Oster, G. & A. W. Pollister, editors. 1955. *Physical Techniques in Biological Research*. Volumes I to III. New York, NY:Academic Press.

Parker, G. H. 1922. The leaping of the stromb (*Strombus gigas* Linn.). *J. Exp. Zool.* 36:205–209.

Perchade, P. L. 1982. A comparison of the *Strombus* (Mollusca) colonies, of two southern Caribbean islands – Trinidad and Grenada. *Caribb. J. Sci.* 18(1/4):35–39.

Randall, J. E. 1964. Contributions to the biology of the queen conch *Strombus gigas*. *Bull. Mar. Sci.* 14:246–295.

Siddall, S. E. 1983. Biological and economic outlook for hatchery production of juvenile queen conch. *Proc. Gulf Caribb. Fish. Inst.* 35:46–52.

_____ . 1984. Synopsis of recent research progress on the queen conch. *J. Shellfish Res.* 4(1):1–3.

Weil M., E. & R. A. Laughlin. 1984. Biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linné in the Archipielago de Los Roques National Park. *J. Shellfish Res.* 4(1):45–62.

Journal of Shellfish Research, Vol. 4, No. 1, 75—104, 1984

ABSTRACTS OF TECHNICAL PAPERS

Presented at 1983 Annual Meeting

NATIONAL SHELLFISHERIES ASSOCIATION

Hilton Head Island, South Carolina

June 6 — 9, 1983

CONTENTS

CONTENTS (Continued)

CONTENTS (Continued)

CONTENTS (Continued)

POPULATION BIOLOGY OF *OCTOPUS BIMACULATUS* VERRILL

AMBROSE, Richard F.,
Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6 Canada.

A 7-year field study of a subtidal octopus population in southern California has provided information on mating behavior, brooding behavior of females on eggs, recruitment, size composition, and population fluctuations of *Octopus bimaculatus*. Mating occurred throughout the year, but there was a distinct seasonality, with most matings observed in May and June. The greatest mating frequency coincided with the initial onset of higher water temperatures. Most females laid eggs from June through August. Water temperature was highest during this period, so development time of the eggs was shortest. Octopuses that laid eggs earlier in the year were much less likely to reproduce successfully. Females stayed with their eggs throughout development and died shortly after the eggs hatched. A year-long study demonstrated that recruitment occurs all year, but there was considerable monthly variability. The size-distribution of adult octopuses changed seasonally due to recruitment and growth of residents. The size of the adult population exhibited cyclic fluctuations that can be explained on the basis of the semelparous life cycle of *O. bimaculatus* and the relatively synchronous initiation of brooding. This general cycle can be severely disrupted, however, by unusually high recruitment in one year.

EVOLUTION OF A *BUSYCON* FISHERY IN THE NEARSHORE SOUTH ATLANTIC BIGHT.

ANDERSON, William D.,
South Carolina Marine Resources Center, Charleston, South Carolina 29412;
EVERSOLE, Arnold G.,
Department of Entomology, Fisheries and Wildlife, Clemson University, Clemson, South Carolina 29631.

The recurrence of poor shrimp harvests since 1977 has led to a diversification of the commercial fleet in South Carolina. Coincident with favorable market conditions and the recognition of abundant whelk populations offshore, shrimpers began to fish for *Busycon carica* (Gmelin) and *B. canaliculatum* (Linne') in the spring of 1978. During the past 5 years this alternative fishery has increased from an annual production of a few thousand bushels in the late 1970's and 1980 to 1982 landings of 37,115 bu. Sublittoral whelk populations are harvested to the greatest extent in the spring by shrimp vessels using either modified otter trawls or crab scrapes. Daily catches of larger vessels often exceed 100 bu. Harvested whelks are processed by hand in South Carolina by removing partially cooked meats from the shells. The meats are transported on ice to markets in New England or frozen and shipped to the Far East.

Whelk fishermen are concerned about maintaining the resource as exploitation increases. In response to this concern, a study has been initiated to gather fundamental biological information to formulate a viable management plan.

WINTER PREDATION BY *ASTERIAS FORBESI* (DESOR) ON COMMERCIALLY IMPORTANT SHELLFISH RESOURCES OF LONG ISLAND SOUND.

AUSTER, Peter J.,
Marine Research Laboratory, The University of Connecticut, P.O. Box 278, Noank, Connecticut 06340.

The literature indicates the common seastar *Asterias forbesi* is a major predator on oyster and mussel beds but also feeds on other available food sources. No mention is made of seasonal variations of prey species in relation to temperature. Diving observations between 1979 and 1983 in Long Island Sound and adjacent waters revealed that *A. forbesi* switched prey species during low temperature regimes (-1.5° to 5°C). Seasonally immotile, temperature-debilitated prey species included *Callinectes sapidus* (Rathbun), *Cancer irroratus* (Say), *Cancer borealis* (Stimpson), *Homarus americanus* (Milne-Edwards), and *Argopecten irradians* (Lamarck). Overwintering concentrations of *C. sapidus* and *A. irradians* have been observed to be heavily preyed upon with greater than 50% of those species observed during survey dives (at 5°C) being attacked. *Cancer irroratus*, *Cancer borealis*, and *Homarus americanus* were observed as prey species but at low percentages and during exceptional circumstances in nearshore habitats. Predation strategy for decapods centers on initial attack at exposed posterior regions (away from chelipeds). Subsequent attacks did not seem to be selective regarding the body region of the prey. Predator-prey interactions are discussed in terms of prey density and behavior at low temperatures.

MASS PRODUCTION FACILITIES FOR THE QUEEN CONCH *STROMBUS GIGAS* (LINNE') AT QUINTANA ROO, MEXICO.

BAQUEIRO, Erik,
Centro de Investigacion y Experimentacion en Maricultura, Can Cun, Quintana Roo, Mexico.

An aquaculture facility that was previously used for the culture of sea turtles has been adapted to produce juveniles of *Strombus*

gigas for release into their natural environment for improvement of the conch fishery. The staff has received training on culture procedures for the queen conch at facilities in Mayguez, Puerto Rico, and Miami, Florida. The first egg masses have been reared under different procedures in order to determine the best techniques for mass culture of the larvae up to metamorphosis. Many doubts exist about the techniques to be used for mass culture of postmetamorphic larvae and juveniles, but the program includes a research protocol to optimize the culture and clarify those doubts that arise.

OCCURRENCE LEVELS OF THE ADDUCTOR MUSCLE PARASITE *SULCASCARIS SULCATA* RUDOLPHI IN THE CALICO SCALLOP *ARGOPECTEN GIBBUS* LINNÉ.

BLAKE, N. J.,
BARBER, B. J.,
RODRICK, G. E.,
Department of Marine Science, University of South Florida, St. Petersburg, Florida 33701.

In late 1981 and 1982 the value of the fishery for the calico scallop *Argopecten gibbus* centered off the east coast of Florida was endangered as a result of the occurrence and recognition of parasites, presumably *Sulcascaris sulcata*, in the adductor muscle. In order to determine the geographic distribution and seasonal occurrence of the parasite along the southeastern coast of the United States, scallops were collected in June 1982 from 16 stations ranging from Savannah, GA, to Fort Pierce, FL. Additional collections were made at 6 of those stations off Cape Canaveral, FL, in December 1982.

Occurrence of at least one parasite per muscle ranged from 28 to 68% ($\bar{X}$ = 40.5%). The internal number of parasites closely followed the number of parasites on the surface of the muscle. A latitudinal pattern of parasite occurrence was not observed; however, levels of parasite occurrence appeared to be related to scallop size and age.

PINNOTHERID CRABS IN BUTTER CLAMS: A COMMENSAL OR A PARASITE?

BOURNE, N.,
Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6.

Pinnotherid pea crabs have been found in several species of British Columbia marine bivalves and are generally considered as commensals in their bivalve hosts. Extensive surveys of British Columbia clam resources have shown that the butter clam *Saxidomus giganteus* (Deshayes) rarely had pinnotherid crabs, but occasionally areas are found where the incidence of crabs in butter clams is significant. In the present study growth rate of butter clams with and without crabs were compared in two areas where there was a significant incidence of crabs in clams. All of the large crabs in the butter clams were female *Fabia subquadrata* Dana, two smaller crabs were male *Pinnixa littoralis* Holmes. Growth rate was significantly slower in those clams with crabs than in clams without than commensals. Factors that cause the erratic occurrence of pinnotherid crabs in butter clams along the British Columbia coast are discussed.

EFFECTS OF SUSPENDED SEDIMENTS ON THE FEEDING PHYSIOLOGY OF THE HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ)

BRICELJ, V. Monica,
Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York 11794.

Suspended sediments, a major component of the seston in estuaries, exert a profound effect on the food availablity and feeding activities of filter-feeding bivalves. Both negative and positive effects on growth have been reported. To determine the effects of suspended sediments on feeding of *Mercenaria mercenaria* (30 mm mean shell length), laboratory studies were conducted using mixed suspensions of algae (*Pseudoisochrysis paradoxa*, Ott, nom. nud. [Clone VA-12]), and bottom sediments (0 to 40 mg·L^{-1}). Effects of silt were tested at three algal concentrations. This study showed that clams were able to sort sediment from algae, and selectively reject both organic-coated and organic-free mineral particles as pseudofaeces. Clams also selectively rejected the larger/heavier mineral particles from a sediment suspension containing a wide range of particle sizes (up to 44 μm in equivalent spherical diameter).

The amount of algae ingested declined with increasing sediment concentrations. This decline resulted primarily from a reduction in clearance rate. Within the range of concentrations tested, clams lost a maximum of about 22% of the algae cleared as pseudofaeces. Pseudofaeces production did not result in a significant loss of algal food at the sediment concentrations normally encountered by clams in the environment. The presence of silt produced no enhancement in the utilization of algae ingested through a so-called "mechanical effect;" however, clams appeared to be able to compensate for the dilution of algae by utilizing a small fraction of the organics in the sediment.

NUTRITIONAL REQUIREMENTS FOR A PATHOGENIC *VIBRIO* SP.

BROWN, Carolyn,
National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460.

The nutritional requirements of a pathogenic *Vibrio* sp. were studied. When grown in a complex, undefined medium, the

bacterium produced a proteinaceous metabolite which was toxic to embryonic development of oyster larvae. A minimal sythetic medium was derived which supported growth of the *Vibrio* sp. but not production of the toxin. A study is currently underway to ascertain the requirements for toxin production.

HARD CLAM PRICE ANALYSIS: THE EFFECT OF SUPPLY AND DEMAND AT THE FULTON FISH MARKET.

BROWN, John W.,
Southeast Regional Office, National Marine Fisheries Service, Charleston Laboratory, P.O. 12607, Charleston, South Carolina 29412.

Prices at the Fulton Fish Market for 3 sizes of hard clams (littlenecks, cherrystones and chowders) were examined for the period January 1973 to December 1982. Prices for the littleneck size were highly seasonal and showed the effect of individual holidays. Prices for the cherrystone size generally followed the prices of the littlenecks with a strong seasonality factor. Chowder prices have generally trended upward and did not show the strong seasonal price changes of the two smaller sizes.

Other factors which affected supply and demand, such as area openings and closures and shellfish transmitted disease events were also examined.

A COMPARISON OF ENVIRONMENTAL PARAMETERS, GENETIC VARIATION, AND LIFE HISTORY TRAITS AMONG LARVIPAROUS AND OVIPAROUS SPECIES OF THE FAMILY OSTREIDAE.

BUROKER, Norman E.,
Bureau of Biological Research, Rutgers, The State University of New Jersey, Piscataway, New Jersey 08854.

The comparison of oyster species from the larviparous group included *Ostrea edulis* (Linné), *O. lurida* (Carpenter), *O. permollis* (Sowerby), and *Tiostrea chilensis* (Philippi) while the oviparous group included *Crassostrea gigas* (Thurnberg), *C. virginica* (Gmelin) and *Saccostrea cucullata* (Born). The life history traits employed in this study were mode of development, adult shell size, breeding season, clutch size/fecundity, egg size, proportion of the population producing eggs or brooding larvae, initial planktonic larval size, planktonic larval period, and larval setting size. The environmental parameters were habitat water depth, habitat water temperature, spawning water temperature, and habitat salinity. The genetic variables include proportion of polymorphic loci per population and proportion of heterozygous loci per individual.

Two multivariant techniques (i.e., correlation coefficients and stepwise multiple-regression analysis) were employed to identify groups of variables that vary in concert and to determine the covariation of genetic variation with environmental parameters and life history traits. Significant correlations were found among 22 of 106 pairwise comparisons. Among environmental variables habitat salinity was found to be inversely correlated to both larval setting size and adult shell size; habitat water depth was inversely correlated to mode of development; habitat water temperature was correlated to planktonic larval period and polymorphic loci; and spawing water temperature was inversely correlated to egg size and initial planktonic larval size. Among life history traits, mode of development was correlated with fecundity, but inversely correlated with egg size and initial planktonic larval size. Levels of genetic variation were found to be correlated with mode of development, fecundity, planktonic larval period, and inversely correlated with egg size and planktonic larval size.

A HABITAT SUITABILITY INDEX (HSI) MODEL FOR THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN) IN THE GULF OF MEXICO.

CAKE, Edwin W., Jr.,
Oyster Biology Section, Gulf Coast Research Laboratory, Ocean Springs, Mississippi 39564;
CORDES, Carroll L.,
National Coastal Ecosystems Team, U.S. Fish and Wildlife Service, Slidell, Louisiana 70548.

An HSI model is described for the American (or eastern) oyster in estuaries along the northern Gulf of Mexico. The model is defined in terms of cultch availability, substrate firmness, mean water salinities, and mean intervals between lethal, freshwater floods. Disease, predation, and other biological variables were excluded as model variables because the model was designed to evaluate the effects of physical habitat changes on carrying capicity.

The model will be utilized by field technicians of the U.S. Fish and Wildlife Service to assess the impact of loss or modification of estuarine habitats occupied or potentially occupied by *Crassostrea virginica* from proposed and/or ongoing water resources development projects. The concept of habitat suitability is defined in terms of expected geographic distributions of oysters and the number of individuals supported by a given unit of bottom area. The general HSI is defined as a ratio of the habitat conditions for a specific study area to the optimum habitat conditions for *C. virginica*. The HSI has a minimum value of 0.0 for totally unsuitable habitats and a maximum value of 1.0 for optimum habitats. The HSI is assumed to be linearly related to carrying capacity to the extent that a change in the index value represents a corresponding change in the potential carrying capacity of the habitat.

DISCRIMINATION OF PREY BY THE ATLANTIC DOGWHELK *NUCELLA LAPILLUS* (LINNÉ)

CARTER, John A.,
Martec Ltd., 5670 Spring Garden Road, Halifax, Nova Scotia, Canada B3J 1H6.

Nucella lapillus is a common predator of barnacles and mussels in the lower intertidal zone of eastern Canada. Although natural diet may reflect food availability to some extent, there is evidence for olfactory discrimination of prey by muricid gastropods which may influence diet under optimal conditions of choice of prey.

Dogwhelks were subjected to metabolites of equal biomasses of the barnacles *Balanus balanoides* (Linnaeus) and juveniles and adults of the blue mussel *Mytilus edulis* (Linne'). Dogwhelks were tested at 4 distances from prey, with different combinations of prey, and with constant switching of prey metabolite tubes to prevent conditioned responses to the tubes. One-hundred and twenty-four potential contacts with prey were analyzed for each prey combination at each distance.

When barnacles and adult mussels were tested together percentage response to adult mussels increased from 1.6% at a predator-prey distance of 1.7 m to 4.8% at 0.3 m. Response to barnacles ranged from 4.8 to 10.5% over the 4 distances. None of these responses was significant compared to controls with no prey. With testing of barnacles and juvenile mussels, there was a significant response of dogwhelks to juvenile mussels at distances of 0.3 to 1.2 m. Response ranged from 4.0 to 63.5% and showed a strict increasing linear relationship with decreasing predator-prey distance. Response to barnacles in this case ranged from 0.8 to 6.5% over the 4 test distances. Juvenile mussels were clearly preferred over adult mussels and barnacles.

Dogwhelks with barnacle-ingestive experience preferred barnacles when adult mussels were the alternative prey, but preferred juvenile mussles when they were the alternative. This suggests an innate preference of juvenile mussels.

Fidelity to originally-contacted prey was very strong. Only 3.8% of dogwhelks switched to the alternative prey when barnacles and adult mussels were tested together; 5.1% switched prey during tests with barnacles and juvenile mussels. This study indicates that dogwhelks can select preferred prey at short distances.

THE EFFECTS OF STARVATION ON SERUM NINHYDRIN-POSITIVE COMPOUNDS (NPC) OF IMMATURE LOBSTERS (*HOMARUS AMERICANUS* MILNE-EDWARDS) AND THE POTENTIAL OF NPC'S AS CONDITION INDICES.

CARTER, John A.,
Martec Ltd., 5670 Spring Garden Road, Halifax, Nova Scotia, Canada B3J 1H6;
DUNPHY, Gary B.,
Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1K6.

Preliminary work on immature lobsters indicated that certain serum amino acids may be sensitive indices of nutritional condition in crustaceans. The preliminary study also identified the responses of essential amino acids to starvation. The concentrations of 39 serum NPC's were measured in immature lobsters (2 mo after molting) at 0, 2, 4, and 6 wk after 1 mo of *ad libitum* feeding to test the hypotheses of the preliminary study.

The total serum NPC concentration (minus urea, which was highly variable) was 1.51 $\mu M \cdot ml^{-1}$ after feeding, increased to 3.06 $\mu M \cdot ml^{-1}$ at 2 wk, and then decreased to 1.76 and 1.69 $\mu M \cdot ml^{-1}$ at 4 and 6 wk, respectively. Proline, glycine, alanine, glutamine, taurine, and serine comprised 60% of the total serum NPC concentration at week 0 and 77% 6 wks after feeding. Individual NPC's showed at least 5 responses to starvation. Orinthine, glycine, and tuarine increased in concentration at 2 wk, then decreased to higher than original levels by 6 wk. B-alanine, methionine, alanine, glutamate, proline, asparagine, glutamine, serine, and aspartate showed the increase at 2 wk, then declined to original levels. Non-essential amino acids were limited to these 2 response categories. Glycine may have compensated for osmotic concentration changes during starvation.

Concentrations of arginine and lysine decreased by the end of the second week, then remained steady. Tryptophan, histidine, phyenylalanine, leucine, isoleucine, valine, and threonine increased in concentration at 2 wk, then showed pronounced declines to below original levels by 6 wk. Apparent essential amino acids comprised these 2 response categories. Only 1-methylhistidine showed a fairly rapid rise to steady levels with increasing starvation. It may serve as a sensitive condition index.

ASSESSMENT OF SUPPLEMENTAL FORMULATED DIETS FOR GROWING SEED OF *MERCENARIA MERCENARIA* (Linne')

CASTAGNA. Michael,
BISKER, R. S.,
Virginia Institute of Marine Science and School of Marine Science, College of William and Mary, Wachapreague, Virginia 23480;
DYMSZA, Henry,
Department of Food Science and Nutrition, University of Rhode Island, Kingston, Rhode Island 02881;

KRAEUTER, John N.,
Baltimore Gas and Electric Company, P.O. Box 1475, Room 1020A, Baltimore, Maryland 21203.

Production of seed clams is a necessary step in the culture of the hard clam *Mercenaria mercenaria*. Growing seed from setting (metamorphosis) to a size that is large enough for field grow out represents a major cost in culture operations. Spawning brood stock and culture of larvae to metamorphosis are relatively efficient operations in most hatcheries; however, the rearing of post-set clams to a sufficient size for grow out is still a problem. The food demands of post-set clams are met by pumping increasing volumes of seawater containing natural food, often supplemented with additions of cultured algae. This technique is costly and often inadequate.

In this study, a number of diets that were formulated from inexpensive agricultural or fishery products were tested for promotion of growth in post-set hard clams. Small clams were selected from a mixed group of hatchery-reared siblings and placed in containers receiving a preset flow of ambient seawater and one diet. The meal-type diets were mixed in a week brine solution and pumped into the test containers at preset rates. Clams were sampled at 1-, 2-, 4-, and 6-wk intervals. Increases in shell height and dry weight were used as indicators of growth. In comparisons between clams that received formulated diets and controls, significantly higher growth rates were observed in clams fed certain diets. These diets are being refined and will undergo further testing.

PROGRESS IN THE DEVELOPMENT OF ARTIFICIAL FOODS FOR OYSTER LARVAE.

CHU, Fu-Lin E.,
WEBB, K. L.,
HEPWORTH, D. A.,
CASEY, B. B.,
Department of Estuarine and Coastal Ecology, School of Marine Science, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062.

Through feeding experiments, the food value of 5 artificial diets used to culture oyster larve have been assessed. These 5 artificial diets were 1) cod liver oil (CLO) and lipid extract of algae in gelatin-acacia walled capsule, 2) CLO supplemented with vitamins B1, B2, and B12 encapsulated in gelatin-acacia, 3) CLO with B vitamin supplements, dextrose, and human albumin encapsulated in lipid, 4) similar to diet 3 with the lipid wall strengthened by incorporating additional ethyl cellulose and saturated fatty acids, and 5) similar to diet 4 but with additional protein (human albumin). Two controls were used, unfed larvae and the *Isochrysis/Pavlova* living algal diet. Oyster larvae were successfully cultured through metamorphosis on diets 1 and 3. Growth rates on the first three diets were the same, but the percentages of "eyed" larvae obtained varied from 0 to 25%. The percentage of survival was much higher than for the unfed larvae. Diets 4 and 5 supported limited growth of oyster larvae. To the best of our knowledge this is the first report of oyster spat produced on non-algal diets.

The number of bacteria in the larval cultures were counted. Growth rate of oyster larvae was not correlated with the number of bacteria present in the larval culture.

A MECHANICAL OYSTER HARVESTER FOR SOUTH CAROLINA ESTUARIES.

COLLIER, J. A.,
McLAUGHLIN, D. M.,
Department of Agriculture Engineering, Clemson University, Clemson, South Carolina 29631.

A mechanical oyster harvester has been developed for intertidal oysters. The harvester is hydraulically powered and mounted on a 16-m steel-hull vessel designed for its operation. The objective of this research was to produce a machine that would efficiently harvest oysters while exerting minimum damage to the oysters and the fragile shell matrix that supports them. Results of 3 years of testing show harvest rates of $18 m^3 \cdot h^{-1}$ (500 $bu \cdot h^{-1}$) with a 3-man crew. Damage to the shell matrix was almost undetectable and about 5% of the harvested oysters were damaged. The harvester can operate at depths of 0.75 to 3.0 m with the head controlled automatically. Bottom contact force is adjustable and regulated automatically during harvesting to minimize bottom damage. The harvesting head can pitch or roll 20^0 to follow bottom contour. Conversion from outboard drive to diesel propulsion is in progress. Eventually the harvester will be used by the State of South Carolina for oyster bed management and transplanting of oysters from polluted areas to public shellfish grounds.

THE EFFECTS OF ENVIRONMENTAL FACTORS ON THE ABILITY OF CHEMICAL CUES TO TRIGGER SETTLEMENT AND METAMORPHOSIS OF THE PACIFIC OYSTER, *CRASSOSTREA GIGAS* (THUNBERG)

COOPER, Ken L.,
SHAW, William N.,
Humboldt State University, Fred Telonicher Marine Laboratory, P.O. Box AE, Trinidad, California 95570.

Eyed larvae of the Pacific oyster *Crassostrea gigas* were expos-

ed to a chemical inducer 3-(3,4-dihydroxyphenyl)-L-alanine (L-DOPA) to determine its effect on metamorphosis and attachment. These tests were conducted under a range of environmental factors (temperature, salinity, light, darkness, and age of eyed larvae). Results to date indicate that in response to L-DOPA, metamorphosis:

1)decreased as temperatures were lowered,
2)decreased at salinities lower than the salinity at which the larvae were reared,
3)increased under constant light compared to constant darkness, and
4)did not significantly increase or decrease within age range examined.

When L-DOPA was added, a number of larvae metamorphosed without attaching. The use of oyster shell as a substrate apparently reduced considerably the effects of L-DOPA on metamorphosis.

TIME-LAPSE VIDEO RECORDING AS A MEANS OF MEASURING ORIENTATION OF THE MILK CONCH *STROMBUS COSTATUS* (GMELIN).

COVICH, Alan P.,
SANDERS, Ilse M.,
Center for Energy and Environment Research, University of Puerto Rico, Marine Ecology Division, Mayaguez, Puerto Rico 00708.

Previous direct visual observations by Sanders suggested that the time required for an individual conch to turn right side up after being overturned (righting behavior) was a useful measure of evaluating water quality. Because of the slowness and variability of some individual's responses, it was efficient to videotape-record righting behavior at intervals and to play back the recorded sequence at faster than real time for analysis. Conchs were undisturbed by movement or sound during video taping because the camera was remote from the recorder and TV monitor. Several conchs were monitored simultaneously and their activity reviewed during "stop-frame" or "single-frame" modes of playback. Increased efficiency allowed more replication within a given time for analysis. Juvenile conchs (6.6 to 7.5 cm shell length) were numbered and monitored during exposure to sublethal concentrations of copper in 24-, 48-, and 96-h bioassays. During pretreatment "control" conchs typically required from 12 to 1200 sec to initiate righting behavior (first opercular kick that moved shell). After 96 h of exposure, this time ranged from 1 min to more than 2 h. Control replication consisted of 3 observations per day for 4 days. Conchs that were exposed to sublethal copper up to 48 h showed rapid recovery of their ability to reorient, but when later exposed for 96 h their recovery during 10 days of observation was significantly slow thus demonstrating an accumulative effect for sublethal copper toxicity.

STATUS OF COMMERCIAL SHELLFISHERIES IN GEORGIA

COWMAN, Charles F.,
Georgia Department of Natural Resources, Coastal Resources Division, 1200 Glynn Avenue, Brunswich, Georgia 31523.

In 1908, Georgia produced over 3.6 x 10^6 kg (8.0 x 10^6 lb) of oyster meats. The industry has been in a gradual decline, bottoming out in 1979 with a mere 5.0 x 10^3 kg (11.0 x 10^3 lb) of meats landed. The reasons for this decline are numerous, but include overharvesting, inadequate management, lack of a unified marketing program, environmental alterations, and pollution. The current landings are hand-picked by approximately 6 firms that harvest from 3 of the 4 approved harvest areas. The amount of acreage available to oyster and clam harvest is severely limited by lack of an adequate Shellfish Sanitation Program and private ownership of most oyster and clam bottoms. Despite the limited available acreage, many out-of-state oyster and clam producers have recently expressed interest in Georgia's shellfish resources.

A summary is presented which includes attempts to remedy the past causes of the industries decline and the state's current program to encourage shellfisheries development.

WATER FLOW OVER AN INTERTIDAL OYSTER REEF AND ITS RELATIONSHIP TO NUTRIENT DYNAMICS.

DAME, Richard,
HASKIN, Elizabeth,
KJERFVE, Bjorn,
Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Georgetown, South Carolina 29440.

A unique method for determining the flux of materials across an intertidal oyster reef is described. The method utilized a 10- to 20-m flume, 1 m wide, which allowed the quantification of water flow. Water velocity was highest at mid-depths and lowest at the surface of the reef. Vertical turbulence and mixing were high and took place across the entire water column within small linear distances. Ebb- and flood-directed flows were very different and can cause considerable edge effects near the ends of the flume. These and other

factors largely influenced the estimation of material fluxes in this system.

PRELIMINARY DATA ON THE USE OF CRAB MEAL AS A SUPPLEMENTAL FOOD FOR JUVENILES OF *MERCENARIA MERCENARIA* (Linné)

DUNCAN, Patricia L.,
CASTAGNA, Michael,
DuPAUL, William D.,
College of William and Mary, Virginia Institute of Marine Science, School of Marine Science, Gloucester Point Virginia 23062.

To date, bivalve nurseries have not been economically feasible. A major reason is the use of cultured algae as the primary food source which is expensive to produce in large quantities. The use of a low cost, supplemental food could alleviate high food production costs.

Commericially available crab meal was tested as a supplemental food for hatchery-reared juvenile hard clams. Two groups of 400 clams each were held in a flow-through, filtered (50 μ), seawater system for 30 days. One group received continuous crab meal supplements while the control group received only maintenance seawater flow. Twenty-six clams, randomly selected from each group, were marked and remeasured on days 5, 10, 15, and 30. More growth was observed in crab-meal fed clams than in control clams. A significant difference (α = 0.05, n = 374) was found between initial and final dry weights in crab-meal fed clams but not in control clams. Final dry weights of crab-meal fed clams were significantly greater (α = 0.05, n = 374) than those of control clams. Overall, the increase in wet and dry weights was 2.5 times greater in crab-meal fed clams than in control clams. This study indicated the potential of crab meal as a supplemental food for juvenile hard clams. Ongoing research is being conducted to determine optimum feeding rates and commerical scale applicability.

BACTERIA ASSOCIATED WITH HEALTHY AND DISEASED OYSTERS IN CHESAPEAKE BAY.

ELLIOT, E. L.,
KEATING, S. T.,
STEMMLER, J.,
COLWELL, A. E. L.,
DECARLO, T.,
COLWELL, R. R.,
Department of Microbiology, University of Maryland, College Park, Maryland 20742.

Oysters (*Crassostrea virginica* [Gmelin]) and surrounding water from several oyster bars in Eastern Bay and the Choptank River were examined for the presence of bacterial pathogens. These studies followed reports of high oyster mortalities in Maryland waters of the Chesapeake Bay and the finding of multinucleated spheres (MSX) in oyster tissues in 1982 in these areas. The purposes of the surveys were to look for bacterial pathogens which could cause or contribute to the oyster mortalities and to determine concentrations of bacterial indicators.

Our studies revealed the presence of fluorescent pigment-producing pseudomonads and arginine-positive *Vibrio* spp. Total and fecal coliforms and *Escherichia coli* (Migula) were found in oysters at 3 sites, but were not detected in the surrounding water. The results were compared with data from previous surveys of some of the oyster bars in these areas and data on bacterial present in oysters during a previous problem with high oyster mortalities associated with the presence of multinucleated spheres.

ISOLATION OF CELL-LINES FROM THE CALIFORNIA MUSSEL *MYTILUS CALIFORNIANUS* CONRAD.

ELLIS, Lehman L.,
BISHOP, S. H.,
Department of Zoology, Iowa State University, Ames, Iowa 50011.

Adult mussels were spawned in the laboratory and the eggs were collected, washed, fertilized, and allowed to develop to straight-hinge larvae. Larval cells were dissociated using trypsinization plus mechanical dispersion, and the resulting cell suspension was plated at 2.0 x 10^5 cells·ml^{-1} in T-25 flasks using an antibiotic-containing medium formulated for the maintenance of embryonic marine bivalve cells. Only after the removal of Amphotericin B from the maintenance medium would cells attach to the culture vessels and divide. Initially, cells were passed at high density (10^7 cells·ml^{-1}), but by the 5th transfers, cells could be passed and grown at lower densities (10^4 cells·ml^{-1}). Light and electron microscopic examinations revealed rounded cells with numerous filopods and variable extoplasmic spreading and aggregation. Testing of cell homogenates using starch gel electrophoresis procedures for various enzymatic markers indicate that the cells were from *M. californianus*. Preliminary karyotyping on cells in the 13-15th passage suggested that they were diploid. The cells represented the first isolation of cell-lines as potentially valuable in toxicological and genetic studies of edible marine bivalves.

PATHOLOGY AND CERTIFICATION OF THE JAPANESE SCALLOP *PLACOPECTEN YESSOENSIS*: A CASE HISTORY.

ELSTON, Ralph A.,
Center for Marine Disease Control, Battelle Marine Research Laboratory, Sequim, Washington 98382;
BURGE, Richard,
Pt. Whitney Shellfish Laboratory, Washington Department of Fisheries, Brinnon, Washington 98320.

Pathological examination in relation to the attempted certification for importation of the Japanese scallop *Placopecten yessoensis* from Mutsu Bay, Amori Prefecture, into Washington State is reported. The species has been imported into California and into a quarantine facility in British Columbia, Canada. To preliminarily determine if the scallop meets the state's import standards for shellfish seed, a presample was examined for infectious pathogens, parasites, and associated predators. The presample consisted of 8 adults (8 cm, S. H.) and 28 juveniles (3 cm, S. H.). Gross examination revealed an attached, yellow, glistening, spheroidal body (3 mm, dia) at the base of the branchial tissue of one juvenile. Histologically, the body was heavily encapsulated, contained apparent ova, and was deeply attached to the gill base by interdigitating fiberous extensions of its tissue. The spheroidal body, according to published accounts, is apparently a parasitic rhizocephalid barnacle, *Sacculina* sp. Infiltrative scallop hemocytes were associated with the parasite. Occasional instances of richettsia-like prokaryotes were observed in gill tissue in several scallops.

Concern about the *Sacculine*-like organism resulted in further evaluation and a determination that the importation of Japanese seed scallops would not be permitted. The presence of these parasites in the seed would probably be a continuing phenomenon; therefore, the culture of F_1 scallops in quarantine facilities is being developed. A pathological examination will accompany such culture efforts. In addition, a novel technique will be utilized in which, native and resident species will be exposed to the new scallop species, in quarantine. Examination of such exposed resident species promises to be an extremely useful method of assessing potential horizontal transmission of infectious diseases from importation candidates to resident species.

GONADAL CONDITION OF *MERCENARIA MERCENARIA* (LINNÉ) IN A SOUTH CAROLINA ESTUARY.

EVERSOLE, Arnold G.,
MICHENER, W. K.,
Department of Entomology, Fisheries and Wildlife, Clemson University, Clemson, South Carolina 29631;
ELDRIDGE, Peter J.,
National Marine Fisheries Service, Southeast Fisheries Center, Charleston, South Carolina 29412.

Gonadal condition (GSI) of clams that were planted at 2 tidal locations and at 3 population densities were evaluated in relation to age, size, sex, season, and culture condition. Changes in GSI reflected seasonal changes in gonadal development. Similar decreases in GSI were observed during the spring (May-June) and fall (September-October) spawning peaks.

The GSI varied significantly ($P<0.001$) with clam size (shell length) and age. Larger clams of the same age had proportionally more gonad tissue than smaller clams. Similarly, older clams had larger GSI than younger clams of the same size. No statistical difference ($P<0.05$) was detected between the GSI of female and male clams of the same age and size.

Clams that were grown at the lowest density level or at the subtidal location were larger and had proportionally more gonadal tissue than clams from high densities or the intertidal location. Size differences between treatments explained the variation in GSI between density treatments, but not between tidal locations. Differences in GSI are discussed in relation to reproductive strategy and plasticity in molluscs.

EFFECTS OF SALINITY ON THE VERTICAL DISTRIBUTION OF THE LARVAE OF *CRASSOSTREA VIRGINICA* (GMELIN) AND *OSTREA EQUESTRIS* (SAY).

FEENY, Craig F.,
Department of Oceanography, Florida State University, Tallahassee, Florida 32306.

The behavior of immature and mature larvae of *Crassostrea virginica* and *Ostrea equestris* that were reared in salinities of 23 and 29‰ was observed in salinities of 17, 23, 29, 35, and 41‰ under stratified and unstratified conditions. The results were tested statistically. Results showed that immature larvae of both species were significantly affected by salinity. Immature larvae of *C. virginica* from common parents, but which were reared in different salinities, displayed similar salinity responses. Immature larvae of *C. virginica* were most abundant in the 29-‰ stratum while immature larvae of *O. equestris* were most abundant in the stratum above that in which they were reared. Among column layers of stratified salinities, mature larvae were at the bottom. Results showed that the concentration of immature larvae above haloclines, as reported in previous research, can be explained by salinity alone.

The salinity at which the larvae were reared had as much influence on the distribution of larvae as did differences in genera. Stratification of spatset of both species in high salinities in the field was not explained by salinity alone. Although *C. virginica* attaches intertidally in high salinities, narcotized larvae of *C. virginica* do not float, even in salinities of 41‰. Salinity effects seem to be more significant in the light than in the dark, suggesting the possibility that characteristically low turbidity of high salinity waters may contribute to the stratification of species in high salinities.

METABOLIC RATES IN FAST AND SLOW GROWING SNAILS

FORD, Susan E.,
Department of Zoology, Duke University, Durham, North Carolina 27706 and Rutgers University Shellfish Research Laboratory, Pt. Norris, New Jersey 08349.

Metabolic rates, measured as oxygen consumption, were examined in fast and slow growing individuals of the pulmonate snail *Helisoma duryi* (Ford) as part of an effort to define some of the physiological mechanisms underlying growth rate differences in molluscs. Snails were raised from hatching and maintained in successive age cohorts that spanned the entire life of the snail. Growth rate variation within any age group resulted in mature snails with up to 12-fold differences in total weight.

Relative growth rates were inferred from same-age snails examined along a size gradient (largest assumed to be the fastest growing) and from same size snails tested along an age gradient (youngest assumed to be the fastest growers). By comparing oxygen consumption rates of snails tested along both gradients, the effects of size and of age on metabolic rates could be determined and distinguished from those associated with growth rate.

Experiments done in this manner under both "routine" and "standard" conditions indicate no measurable association of oxygen consumption with growth rate in this species.

SELECTIVE FEEDING AND GRAZING RATES OF LARVAE OF THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN) ON NATURAL PHYTOPLANKTON ASSEMBLAGES IN DELAWARE BAY.

FRITZ, Lowell W.,
FOOTE, M. A.,
VAN DOVER, C. L.,
LUTZ, R. A.,
Department of Oyster Culture, NJAES, Cook College, Rutgers University, New Brunswick, New Jersey 08903,
EWART, J. W.,
College of Marine Studies, University of Delaware, Lewes, Delaware 19958.

Result of laboratory feeding experiments suggest that small phytoplanktonic organisms ($< 10\mu m$) are selected by oyster larvae over larger forms, but that little selection occurs within this small fraction. Experiments were conducted in 1000-ml volumes of 44-μm-filtered Delaware Bay water (filtered to remove zooplankton and wild larvae). Cultured larvae (mean sizes of 71, 126, and 136 μm) were added to experimental containers at densities of 1, 8, and 25 ml^{-1}. Experiments were terminated after 6 and 24 h.

Within the small phytoplankton fraction, larvae grazed upon each of 5 groups encountered (coccoids, centrate diatoms, pennate diatoms, dinoflagellates, and flagellates) at rates proportional to phytoplankton group densities in control cultures. This suggests that larvae were not selectively feeding upon any of the 5 small phytoplankton groups. Larval grazing rates also declined with increases in both larval density and experimental duration, indicating that phytoplankton densities were reduced to levels below those necessary for sustaining high feeding rates. Larval densities employed in experiments were many times higher than natural densities in Delaware Bay (highest densities $=0.2$ ml^{-1}). At experimental densities of 1 larva ml^{-1}, percent declines of all small phytoplankton groups relative to the controls averaged only 3%. The impact of oyster larval grazing on phytoplankton population densities in Delaware Bay should be minimal.

GENETIC ASPECTS OF ENERGY METABOLISM DURING STARVATION IN THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN).

GAFFNEY, Patrick M.,
RODHOUSE, Paul G.,
KOEHN, Richard K.,
Department of Ecology & Evolution, State University of New York at Stony Brook, Stony Brook, New York 11794.

Correlations between multiple-locus heterozygosity at electrophoretically detected enzyme loci and growth rate have been demonstrated in variety of organisms, including the American oyster *Crassostrea virginica*. Although no satisfactory physiological or biochemical explanation of this phenomenon exists, experiments with American oysters indicate a correlation between multiple-locus heterozygosity and metabolic rate as determined from measurement of oxygen consumption.

Data collected during recent experiments are presented on the relationships between oxygen consumption, ammonia excretion,

glycogen depletion, and heterozygosity. The relevance of the findings to mariculture, particularly selection of hatchery broodstock, is discussed.

LIPIDS AND THE CONDITION OF MARINE BIVALVE LARVAE.

GALLAGER, Scott M.,
MANN, Roger,
Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

Neutral lipids, predominantly triacylglycerides, are an important energy reserve in the larvae of *Crassostrea virginica* (Gmelin), *Mercenaria mercenaria* (Linné), and *Ostrea edulis* (Linné) and are metabolized under stress. Small fluctuations in total lipid levels in individual larvae due to adverse culture conditions such as thermal or nutritional stress were in the range of 2 to 10 ng of lipid per larva. A practical index of larval condition based on the variability in lipid content between individual larvae can be obtained by staining larvae specifically for lipid and subsequent microscopic examination. Subsamples from cultures can be compared to a set of reference photographs illustrating the effect of known environmental conditions on stained lipid reserves.

Data from our laboratory and two commerical hatcheries rearing *M. mercenaria* and *C. virginica* suggest that a threshold relationship exists between egg lipid content and subsequent larval growth and metamorphosis. Under otherwise identical culture conditions, eggs with a high lipid content give rise to larvae in better condition and which complete metamorphosis with a higher degree of success than eggs with a low lipid content. Lipid levels in 24-h straight-hinge larvae, visualized with lipid-specific stains, may be used as an index of potential culture success. The possible existence of an energy threshold level in pediveliger larvae that is necessary for successful metamorphosis is discussed.

COMPARISON OF ENERGETICS OF HARD CLAM PREDATION BY *NEOPANOPE SAYI, OVALIPES OCELLATUS*, AND *PAGURUS LONGICARPUS*.

GIBBONS, M. C.,
Virginia Institute of Marine Science, Wachapreague, Virginia 23480.

Juveniles of the hard clam *Mercenaria mercenaria* (Linné) are susceptible to predation by crabs, gastropods, and starfish. These have generally been considered exceptionally "voracious" predators, consuming 20-25% of their own live body weight per day. The bioenergetics of ingestion, absorption, and respiration were used to examine the voracity of hard clam predation by the mud crab *Neopanope sayi* (Smith), the calico crab *Ovalipes ocellatus* (Herbst), and the hermit crab *Pagurus longicarpus* Say. Crabs were several orders of magnitude more voracious than starfish or gastropods in terms of ingestion rate (# clams·predator^{-1}·day^{-1}). On the basis of body-weight (%) comparisons of the prey consumed per day, however, adult crabs, starfish, and snails consumed similar amounts of prey. Predatory gastropods and starfish have long search and attack procedures to pursue their prey. They have specialized diets and generally prey on relatively large prey. Crabs are searchers, do not extensively pursue individual prey, have more flexible diets, and consume large numbers of small prey daily. The ingestion rates of predators are influenced by their metabolic rates and their ability to convert food into net energy. *Neopanope sayi*, *O. ocellatus*, and *P. longicarpus* have high absorption efficiencies and metabolic costs compared to predatory gastropods. The crabs lost larger percentages of energy via respiration than predatory gastropods. These data are consistent with the differing methods of foraging used by crabs and predatory gastropods.

PREDATION OF JUVENILES OF THE HARD CLAM *MERCENARIA MERCENARIA (LINNÉ)* BY FIFTEEN INVERTEBRATE SPECIES WITH SPECIAL REFERENCE TO CRABS.

GIBBONS, M. C.,
Virginia Institute of Marine Science, Wachapreague, Virginia 23480.

In laboratory feeding studies, invertebrate species were offered different sizes of juvenile hard clams (*Mercenaria mercenaria*) as prey. Fifteen of the 19 species tested were observed to consume juvenile hard clams. Crabs had higher predation rates than gastropods, shrimp, and starfish. Clam predation by crabs was influenced by variables such as clam size, crab size and species, temperature, and substrate. Crabs preyed upon hard clams with shell lengths up to 30% of their carapace widths. The size of prey affected the predation method used by crabs. Predation decreased with declining temperature and resumed when water temperature rose in the spring. The rock crab *Cancer irroratus* Say, however, was observed to prey on hard clams at a seawater temperature of 0°C. Substrate type influenced predation. Crushed gravel aggregate and to a lesser extent sand provided protection for juvenile hard clams against predation by *Neopanope sayi* (Smith), *Ovalipes ocellatus* (Herbst), and *Pagurus longicarpus* Say.

SIMPLE CULTURE METHODS FOR PLANKTOTROPHIC AND NONPLANKTOTROPHIC BIVALVE LARVAE

GOODSELL, Joy G.,
LUTZ, R. A.,
Dept. of Oyster Culture, NJAES, Cook College, Rutgers Univ., New Brunswick, New Jersey 08903;
CASTAGNA, M.,
VIMS, Wachapreague, VA, 23480.

In the course of recent morphological investigations on a variety of bivalve larvae, we spawned adults and cultured the larvae (planktotrophic and nonplanktotrophic) of a variety of boreal, temperate, and tropical species. Adult and larval stages were held in 20-*l* containers of clarified seawater without aeration. Larval culture containers were changed on alternate days and temperatures were maintained using water baths. Adults, juveniles, and planktotrophic larvae were fed a raw seawater concentrate consisting of suspended organic and inorganic particles that pass through a 10-μm bag filter. Particulate matter from thousands of liters of filtered seawater was concentrated into a thick paste with a continuous flow centrifuge. The paste was resuspended in a small volume of seawater and refrigerated. With frequent agitation, the food was capable of refrigerated storage for several weeks. (In addition to its value for larval nutrition, the concentrate may be used, in conjunction with thermal and gonadal stimulation, to induce spawning in some species.) The remaining particle-free seawater provided a suitable culture medium for rearing the larval stages of species with lecithotrophic development; to date the larval stages of *Astarte castanea* Say, *Periploma leanum* (Conrad) and *Cyclocardia borealis* (Conrad) have been successfully reared utilizing this supernatant. When this technique was employed, a variety of species (having either planktotrophic or nonplanktotrophic modes of development) can be successfully raised without an extensive algal culture facility.

ECOLOGICAL STUDIES OF *OCTOPUS DOFLEINI* (WÜLLER) ON THE WEST COAST OF BRITISH COLUMBIA

HARTWICK, Brian,
Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6.

Tagging studies, trapping, and observations have contributed to our understanding of the life history and ecology of the common Pacific octopus *Octopus dofleini*; however, critical questions remain unanswered. These questions will be identified and results from recent field studies will be discussed in relation to them. Areas of special interest include den limitation, early benthic stages, and migration behavior.

FOOD AVAILABILITY AND FEEDING PREFERENCES OF THE QUEEN CONCH *STROMBUS GIGAS* (LINNÉ) COLLECTED FROM NATURAL HABITATS.

HENSEN, Roberto,
Carco Project, P. O. Box 43, Bonaire, Netherlands Antilles.

This was a study of habitats which support the queen conch *Strombus gigas*, the availability of potential foods for conchs in those habitats, and the preferential intake of those foods by these molluscs. Large populations of conchs were studied *in situ* in the Bahamas, Columbia, and Netherlands Antilles, and stomach analysis of approximately 900 conchs from 17 sites were compared with food availability at those sites. Using electivity formulas, it was shown that within high levels of probability conchs select for microalgae, detritus, and fine filamentous macroalgae. Juvenile conchs tended to concentrate in large numbers in shallow waters near beds of seagrasses. They ingested mostly particles less than 4 mm^2 of which the microalgae fraction was assimilated preferentially. This was due to anatomical characteristics of the alimentary tract.

EVOLUTION OF THE GREAT SOUTH BAY SHELLFISH INDUSTRY.

KASSNER, Jeffrey,
CRAMER, Thomas, W.,
Department of Environmental Protection, Town of Brookhaven, Patchogue, New York 11772.

The Great South Bay on Long Island, N.Y., has long been a leading producer of shellfish in the United States. During the past 180 years, however, the resource and its fishery have undergone dramatic change shifting from the American oyster *Crassostrea virginica* (Gmelin) to the northern hard clam *Mercenaria mercenaria* (Linné). This resulted from changes in both the management of shellfish and the hydrography of the bay. In the early 1800's, the Bay supported a sizeable oyster fishery but overfishing and oyster dredging depleted the natural beds by 1870. Beginning in 1880,

oyster production increased as large areas of the bay were leased for oyster planting. Because of political pressure and court action that gave 5,666 ha (14,000 a) of formerly public bay bottom to a private company, leasing was largely discontinued after 1900. Between 1910 and 1940, salinities in the bay increased markedly due to changes in flow through Fire Island Inlet and the opening of Moriches Inlet in 1931. As a result, the oyster drills *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) increased in abundance and few oysters survived past setting. In the 1940's, dense blooms of a small flagellate that interfered with oyster feeding, caused a further decline in oyster abundance, No significant oyster fishery existed after 1948. The conditions that were detrimental to the oyster proved beneficial to the hard clam, which increased in abundance. Hard clam production increased rapidly, peaking at 24,668 m^3 (700,000 bu) in 1976. Landings have since declined by half as a result of overfishing and further changes in the bay. A variety of management programs are now being used to stabilize landings.

EFFECTS OF A MECHANICAL OYSTER HARVESTER ON MACROBENTHIC COMMUNITY STRUCTURE.

KLEMANOWICZ, Kathryn J.,
Grice Marine Biological Laboratory, College of Charleston, Charleston, South Carolina 29412;
STEELE, George H.,
Marine Resources Research Institute, Charleston, South Carolina 29412.

The ecological effects of mechanical harvesting on the interidal benthic invertebrate community associated with oyster beds in Beaufort County, SC, is being studied. At a harvest site macrobenthos that inhabit oyster beds in the high and low intertidal zones are being monitored before and after harvesting and at seasonal intervals over an annual cycle. In order to assess changes in community structure that may be effected by the harvester, a nearby control will be sampled on the same schedule as the harvested site.

For each sampling period, a 16-m^2 circular quadrat is being used to collect 5 replicate samples from both high and low intertidal areas in the harvested and control sites. A quantitative assessment of motile and noncolonial macrobenthos is being made, whereas only the species composition of colonial and encrusting organisms is noted. Biomass is determined for all live oysters in a sample in addition to other molluscs (including shell) and decapod crustaceans. Changes in diversity, species composition, and relative density are being analyzed for the macrobenthic commmunity inhabiting intertidal strata at each site. Information gained will be used to determine whether the integrity of the benthic community is disturbed by use of the mechanical harvester.

COMPARISON OF GROWTH INCREMENT AND STABLE ISOTOPE AGE DETERMINATION METHODS FOR THE ATLANTIC DEEP-SEA SCALLOP, *PLACOPECTEN MAGELLANICUS* (GMELIN)

KRANTZ, David E.,
Marine Science Program, University of South Carolina 29208;
JONES, Douglas S.,
Department of Geology, University of Florida, Gainesville, Florida 32611;
WILLIAMS, Douglas F.,
Belle W. Baruch Institute of Marine Biology and Coastal Research, University of South Carolina, Columbia, South Carolina 29208.

Accurate models for age determination in commercially harvested molluscs are important for resource assessment and managment. Present aging techniques for deep-sea scallops (*Placopecten magellanicus*) use interpretations of external growth checks on the shell extrapolated from mark and recovery studies. Although these methods are simple and inexpensive, the assumption that external growth checks represent annual events may not hold true in all cases. Our results show that the stable oxygen isotope composition of mollusc shell carbonate provides an independent method for interpreting low-order growth increments. Records of $\delta^{18}O$ from serially sampled carbonate powders show annual cycles of ambient temperature changes,and provide an externally controlled time scale. We obtained for analysis several specimens of *P. magellanicus* collected alive from 60 m water depth off the coast of Virginia. Two specimens which were aged using external growth checks were assigned ages of 3 and 7 y. Stable isotope profiles of these 2 scallops reveal only 2 and 4 annual cycles respectively. The discrepancy between the results using these two methods may have important implications for the determination of age structure and resource management of harvestable scallop populations.

AN EVALUATION OF THE USE OF POLYMERIC XAD RESINS IN THE TREATMENT OF FOULED SEAWATER FOR BIVALVE LARVAL CULTURE.

LANGDON, Christopher J.,
SIEGFRIED, C. A.,
College of Marine Studies, University of Delaware, Lewes, Delaware 19958.

Bivalves larvae that were grown in seawater that had been fouled by the feeding and metabolic processes of adult bivalves, grew com-

paratively less than animals grown in fresh seawater. Amberlite XAD 2, 4, 7, and 8 resins (Rohm and Haas) were used at concentrations of 0.1, 1 or 10 gm L^{-1} (dry wt) in the batch treatment of the fouled seawater in an attempt to improve it's quality. Water quality was assessed by determining (a) the proportion of fertilized eggs which developed normally to D-stage larvae and (b) larval growth over a 6-day period. Treatment of fouled water with concentrations as high as 10 gm L^{-1} resin did not adversely effect the proportion of fertilized eggs which successfully developed into D-stage larvae. Larval growth in fouled water which had been treated with the lowest concentration of XAD resin tested (0.1 gm), was improved compared with that of larvae grown in non-treated, fouled water. The growth of larvae in fouled water which have been treated with XAD 2 resin at 0.1 gm was not significantly different (SNK range test, $P < 0.05$) from that of larvae cultured in fresh seawater. The authors discuss the potential use of XAD resins for seawater treatment in intensive bivalve culture systems.

THE USE OF CALCIUM ALGINATE MICROCAPSULES IN THE STUDY OF THE NUTRITIONAL REQUIREMENTS OF LARVAE OF THE MUD CRAB *EURYPANOPEUS DEPRESSUS* (SMITH).

LEVINE, Daniel M.,[1,2]
SULKIN, Stephen D.,[1]
VAN HEUKELEM, Lauie,[1]
SELZER, Jonathan A.[1]
University of Maryland, Horn Point Environmental Laboratories, Box 775, Cambridge, Maryland 21613,
University of Maryland, Department of Zoology College Park, Maryland 20742.

Larvae of the mud crab *Eurypaneous depressus* that were fed brine shrimp nauplii showed enhanced survival and rate of development over larvae that were fed rotifers that had been cultured on the alga *Dunaliella tertiolecta* (Butcher). We hypothesized that larvae required essential polyunsaturated fatty acids that were present in the brine shrimp but not in the rotifers. To test this hypothesis, we encapsulated both brine shrimp lipid and specific polyunsaturated fatty acids (18:2ω6, 18:3ω3, 22:6ω3) using a calcium alginate system. We supplemented the living rotifer diet with the appropriate encapsulated lipid. Our experiments demonstrated that when the rotifer diet was supplemented by brine shrimp lipid, survival and rate of development approximated that observed on a diet of living brine shrimp nauplii. A similar result was obtained when the rotifer diet was supplemented with the PUFAs listed above.

MOLLUSCAN SHELL DISSOLUTION AT DEEP-SEA HYDROTHERMAL VENTS: IMPLICATIONS FOR DETERMINING GROWTH RATES OF ABYSSAL MOLLUSCS

LUTZ, R. A.,
Department of Oyster Culture, New Jersey Agriculture Experiment Station, Cook College, Rutgers University, New Brunswick, New Jersey 08903.

Direct measurements of molluscan shell dissolution at the 21°N hydrothermal vent fields along the East Pacific Rise have revealed marked differential dissolution of various shell microstructures. Shell fragments of two species of bivalve molluscs, *Calyptogena magnifica* (Boss and Turner), a vesicomyid, and a presently unclassified mytilid that have been encountered at numerous submarine hydrothermal vent areas were embedded in an epoxy resin, radially sectioned, and finely polished. Using DSRV Alvin the polished sections were placed on 14 Nov 1981 within an area of hydrothermal activity at a depth of 2618 m and retrieved 161 days later. The mean thicknesses of the dissolved shell material, as determined from measurements of differential relief from the polished epoxy surfaces, may be summarized as follows for the various shell layers of the two species: (1) *Calyptogena* (entirely aragonite)- outer granular, 88 μm; middle fine to irregular compex crossed lamellar, 82 μm; pallial myostracum, 67 μm; adductor myostracum, 23 μm; inner cone complex crossed lamellar, 76 μm; (2) mytilid - outer fibrous prismatic calcite, not measureable (< 1 μm;) dissolution; middle and innernacreous (aragonite), 67 μm; pallial myostracum (aragonite), 24 μm.

Through detailed analyses of consistently-oriented shell section of *Calyptogena* that were alive at the time of sampling, the amount of outer shell layer dissolved at any distance from the umbo can be determined precisely. Assuming a constant rate of dissolution (approximately 200 $\mu m \cdot yr^{-1}$ for the outer shell layer), these measurements may be utilized to calculate accurately the growth rates and age structure of *Calyptogena* in the studied environment. Moreover, the technique provides a potentially powerful new ecological tool for assessing growth of numerous other calcium carbonate-secreting organisms located below either calcite or aragoite compensation depths in the deep-sea environment.

NATURAL SURVIVORSHIP OF YOUNG HARD CLAMS, *MERCENARIA MERCENARIA* (LINNÉ) IN EASTERN LONG ISLAND SOUND

MALINOWSKI, Steve M.,
WHITLATCH,R. B.
University of Connecticut, Marine Research Laboratory, Noank, Connecticut 06340.

Experimental field manipulations were used to determine the natural survivorship of *Mercenaria mercenaria* during the first 3 y of life at 2 sites in eastern Long Island Sound: a small protected inland estuary (Poquonock River, Groton, CT) and an exposed, outer harbor (West Harbor, Fishers Island, NY). Clams were planted and recovered at both monthly and full season intervals from May 1982 through November 1982. Three densities (25, 150, and 300 clams per 0.25 m^2) and 6 sizes (1, 5, 10, 15, 18, and 21 mm) were tested.

More than 99% of the mortality at both sites was the result of crustacean predators. Green crabs (*Carcinus maenas* [Linnaeus]) were the dominant predators of clams up to 10 mm while lobsters (*Homarus americanus* [Milne-Edwards]) readily consumed 15- to 21-mm clams. The full season survival of all size classes was consistently higher in the estuary than at the outer harbor site (13, 12, 83% versus 10, 7, and 42% for 1st, 2nd, and 3rd year clams). The dramatic difference between the survival of 3rd year clams at the two sites was attributed to the absence of lobsters in the Poquonock River. The results of monthly experiments revealed complex seasonal components to the rates of predation as a function of both clam size and site. Significantly different patterns were observed for different size classes of clams that were planted at the same site as well as similar size classes planted at different sites. Survival was strongly density dependent, particularly in West Harbor where the mean monthly survival of 5- and 10-mm clams that were planted at the lowest density was more than 4 times higher than the survival of clams planted at the highest density.

Any hard clam resource management program that attempts to supplement natural populations must take into consideration seed-clam planting size, density, and season, as well as the unique site-specific interactions of these factors.

COMMERCIAL-SCALE, UPFLOW NURSERY CULTURE OF THE NORTHERN HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ) IN SOUTH CAROLINA

MANZI, John J.,
MADDOX, M. B.,
STEVENS, F. S.,
Marine Resources Research Institute, Charleston, South Carolina 29412;
CLAWSON, H. Q. M.,
Trident Seafarms Co., Charleston, South Carolina 29401.

Mollusc nursery systems in the United States have traditionally utilized raceway culture techniques although upflow culture has received sporadic attention, particularly over the last 10 y. Recently, a commercial-scale nursery, employing upflow technology exclusively, has been constructed in conjunction with the Marine Resources Research Institute/Trident Seafarms Company cooperative hard clam mariculture project in South Carolina. The nursery consists of 60 forced upflow silos (20-cm diameter) used for initial growth of imported, 1-mm seed and 120 passive upflow silos (55-cm diameter) used for seed growth from ~ 3 mm to field planting size (~ 8 mm). At full operation the nursery requires a minimum total flow rate of ~ 5,000 $L \cdot min^{-1}$, has a holding capacity of 24 x 10^6 seed, and an optimum annual production capacity of 18 to 36 x 10^6 planting size seed. This paper presents construction details of the passive and forced upflow systems and protocols for nursery operations. Data generated from experimental-scale, upflow systems operating in coincidence with the commercial nursery indicated favorable comparisons with raceway data based on water use per unit biomass supported and biomass support capacities per unit area.

IS THERE A TERMINAL MOLT IN ADULT FEMALE BLUE CRABS?

McCONAUGHA, John R.,
Department of Oceanography, Old Dominion University, Norfolk, Virginia 23508.

Classical theory suggests that for female blue crabs (*Callinectes sapidus* Rathbun) the molt to puberty is a terminal molt. Bilateral eyestalk ablation on adult female crabs resulted in the onset of pro-ecdysis and culminated in attempted ecdysis 2 to 3 weeks later. This indicated that adult females were physiologically capable of undergoing ecdysis. The presence of developing limb buds on crabs taken from Virginia's winter dredge fishery and occasional reports of "red-sign" adult females raises questions about the terminal molt hypothesis.

MOVEMENT AND ACTIVITY OF *OCTOPUS DOFLEINI* (WÜLKER) MONITORED BY SONIC TRACKING.

MATHER, Jennifer A.,
Department of Psychology, The University of Western Ontario, Canada N6A 5C2;
RESLER, Steven C.,
Environmental Analyst, Smithtown N.Y.;
COSGROVE, James A.,
Department of Biology, University of Victoria, Victoria, Canada.

Four individuals of *Octopus dofleini* were marked with sonic tags and their movement monitored over 2 weeks in Saanich Inlet, BC. Octopuses had small home ranges, 250 m^2, over this period. The home ranges overlapped considerably and there was no evidence of spacing at constant distance, which suggests that the octopuses were solitary and asocial. Animals were more active at night but only statisically so. Trips, presumably to hunt, were frequent and short, with a mean of over 1 h and mode of 0.5 h. They were more likely to be longer at night. The adaptability of this pattern to the life style of a solitary predator will be discussed.

METAMORPHOSIS OF *STROMBUS GIGAS* (LINNÉ) AND *APLYSIA BRASILIANA* (RANG) IN LABORATORY CULTURES.

MIANMANUS, Ratsuda,
Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149.

A comparative study of the metamorphosis of the queen conch *Strombus gigas* and the sooty sea-hare *Aplysia brasiliana* was conducted. Competent larvae of both species settled and metamorphosed on red macroalgae. Seawater extracts of red algae induced shedding of velar cilia signalling onset of metamorphosis. Larvae of *S. gigas* responded at a relatively lower concentration of extract than did larvae of *A. brasiliana*. Preliminary studies suggested that the biologically active component of the algal extract is phycoerythrin.

CONTRIBUTIONS TO THE REPRODUCTIVE BIOLOGY OF *ARCA ZEBRA* (SWAINSON) IN SUCRE STATE, VENEZUELA.

NAKAL, Alberto,
PRIETO, A.,
Department of Biology, Universidad de Oriente, Cumana, Venezuela.

Individuals of *Arca zebra* were sampled over a 3-year period in different areas of Sucre State, eastern Venezuela. Gonadal development was determined histologically and related to the ark size and wet meat weight. A 5-stage scale of sexual maturity was established for both sexes based on follicle diameter and number, quantity of mature elements, and thickness of germinal epithelium. Ovocyte diameter varied between 30 and 160 μm in the different stages. Most individuals between 20 and 40 mm in length were males. Hermaphrodites, when found were larger, suggesting a sexual inversion or synchronous hermaphroditism. Environmental parameters with which gonadal development was associated were studied. Temperature was highest in October (27°C) and lowest between December and January (21°C). Salinity varied from 35.8 $^{0}/_{00}$ in August to November to 34.0 $^{0}/_{00}$ in January. Effects of dissolved oxygen and the coefficient of light extinction were also studied.

QUALITY CONTROL AND MAINE MUSSELS.

NEWELL, C. R.,
Research and Development, Great Eastern Mussel Farms, P.O. Box 141, Tenants Harbor, Maine 04860.

The rapidly developing Maine mussel industry is currently based primarily on the harvest of select wild and bottom-cultured mussels. Quantitative mussel quality characteristics were developed and used as criteria for the selection of high quality wild mussels, to develop a grading system, to select seed for bottom culture, and to time harvesting activities for maximum meat yields. Mussel quality may be defined in terms of steamed meat yield, pearl incidence, shell appearance, shelf life, and mussel size. Steamed meat yield is determined by steaming 25 to 30 mussels under constant conditions, draining, and dividing steamed meat weight by total steamed weight. Total steamed weight is used in the denominator instead of total wet weight because of the variability in total wet weight (about 20%) due to amounts of enclosed water. Pearl incidence is determined from meats dissolved in a 5% (by weight) solution of potassium hydroxide and poured through a 1.1-mm diameter sieve. The results are presented as the number of mussels per detectable pearl or the number of pearls per gram of steamed meat. Taste panel studies are needed for a realistic definition of detectable pearl size. Shell appearance is defined as black or eroded, thin or thick. Shelf life is determined as the percent mortality (gapers) of approximately 100 mussels that were held in perforated plastic bags at 5°C (41°F). Shelf life is terminated when 7% of the sample is gaping. Mussel size is presented as the mean shell length (mm) and meat weight (g). Mussel quality criteria are also useful for regulating bottom densities on the culture beds and for selecting seed with low pearl incidence and good shell appearance.

SEASONAL GROWTH, GLYCOGEN CYCLE, AND ANNUAL GROWTH-LINE FORMATION IN THE SOFT-SHELL CLAM *MYA ARENARIA* LINNÉ

NEWELL, C. R.,
Program in Oceanography, University of Maine at Orono, Ira C. Darling Center, Walpole, Maine 04573.

The seasonal growth, glycogen cycle, and timing of the formation of the annual growth line in the inner shell layer of hatchery-reared juveniles and wild adults of *Mya arenaria* were followed for one year. The most rapid growth and highest glycogen levels occurred in the spring and early summer in Maine. Growth lines in the inner shell layer of juvenile and adult clams were formed in the months of March and April. Clams began forming the line in late winter when tissue glycogen levels were the lowest. Smaller clams finished forming the annual line earlier in the spring than larger clams from the same intertidal level, and clams from mean low water finished growth-line formation earlier than clams of similar size from the upper shore.

THE INFLUENCE OF ENVIRONMENTAL FACTORS AND THE PARASITE MSX ON THE PHYSIOLOGY OF THE OYSTER *CRASSOSTREA VIRGINICA* (GMELIN).

NEWELL, Roger I. E.,
Horn Point Environmental Laboratories, University of Maryland, Cambridge, Maryland 21613.

The results of ongoing research on the American oyster *Crassostrea virginica* under ambient field conditions indicate a pronounced seasonal cycle of all measured physiological rate functions (*viz* metabolic rate, clearance rate, absorption efficiency, and ammonium-nitrogen excretion) which is typical of other bivalves from shallow temperate waters. It seems likely that these cycles are due to both seasonal variations in endogeneous factors, associated with reproduction, and exogeneous factors, dominated by water temperature and food availability. A balanced energy budget, constructed by integrating these variables, indicates that there is a pronounced seasonal cycle in energy available for growth and reproduction. This normal seasonal pattern can be severely disrupted, however, by short-term stochastic events. For example, salinities below $10^0/_{00}$ depress the feeding rate of oyster, including those collected from localities with ambient salinities always below $10^0/_{00}$ compared to their rates measured at $20^0/_{00}$. Recent preliminary research also indicates that the oyster parasite MSX (*Haplosporidium nelsoni* Haskin, Stauber, and Mackin) can also have a significant effect on the energy budget of *C. virginica* by depressing feeding rates. The condition indexes of these MSX-infected oysters were reduced by 36% compared to control oysters.

PROTEIN REQUIREMENT OF JUVENILE LOBSTER, *HOMARUS* SP.

NORMAN-BOUDREAU, Karen E.,
CONKLIN, D. E.,
Aquaculture Program, Bodega Marine Laboratory, University of California, P.O. Box 247, Bodega Bay, California 94923.

Replicate groups of 60-day-old lobsters were fed *ad libitum* on artificial diets varying in protein from 0 to 53% for 90 days. Casein or casein/shrimp protein (tail meat only) mixtures were the two protein sources utilized and cornstarch was substituted when varying protein levels. Live *Artemia* and protein-free groups served as controls. Results indicated that protein levels in the diets were directly related to increases in dry and wet weights and all groups had excellent survival. Lobsters that were fed casein/shrimp protein mixtures grew better at lower protein levels than did their counterparts receiving only casein. Growth rate per unit protein was best at 18% casein/shrimp or at 23% casein for the two protein sources. No detrimental effect of high protein level was noted; however, at levels > 30% little increased benefit was noted. These results are important in light of current dietary practices in shrimp and lobster cultures of providing > 30% of the diet as protein.

EFFECTS OF TEMPERATURE ON THE EMBRYONIC DEVELOPMENT OF THE NORTHERN PINK SHRIMP *PANDALUS BOREALIS* KROYER.

NUNES, Pepsi,
NISHIYAMA, T.,
Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99701.

Temperature effects on embryonic development were examined to assess how it may contribute to fluctuations in abundance of shrimp populations. Ovigerous shrimp were kept at temperatures reflecting the range of temperatures encountered in their natural environment. At the upper end of the temperature scale, differences in temperature had relatively little effect on development, whereas at the lower end temperature differences resulted in more pronounced effects. While egg development was prolonged at 3°C, the acceleration of development rate from organogenesis to hatching through the range of temperatures from 3 to 9°C was not uniform but increased gradually at 3°C, resulting in a progressive relative

increase in reaching these later stages at higher temperatures. There was no correlation between shrimp size and rate of embryonic development. Increases in egg size with incubation period were inversely related to their original size and the length of their incubation period. The influence of temperature on the growth rate of developing embryos was accentuated in the later embryonic stages at the lower temperatures. The highest incidence of egg loss during the incubation period occurred among shrimp at 3°C. The occurrence of marked egg loss at 3°C suggested that the availability of higher temperatures played a role in defining distributions of spawning populations. The percentages of total egg hatch and viable larvae produced were examined in relation to incubation temperature. Total hatch and viable hatch were highest at 3°C. The greatest numbers of viable larvae of largest size at yolk exhaustion occurred at 3°C. Temperature regimes during the incubation period have profound effects on the numerical strength and viability of the resulting year-class.

EFFECTS OF TEMPERATURE AND FOOD AVAILABILITY ON THE SURVIVAL AND GROWTH OF LARVAE OF THE NORTHERN PINK SHRIMP *PANDALUS BOREALIS* KROYER

NUNES, Pepsi,
NISHIYAMA, T.,
Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99701.

The relationship between larval survival and food availability was examined at ecologically meaningful temperatures to assess how these environmental factors affected larval recruitment success. Larvae that were hatched from eggs incubated at different temperatures were reared to early juveniles at different temperatures and feeding levels (satiation, adequate or marginal diets of *Artemia* nauplii, and algae). Rearing temperatures had the greatest effects on larval survival. Survival to metamorphosis was consistently highest for larvae that were grown at 9°C at all levels of feeding. Larvae that were hatched from eggs incubated at 3°C tended to have highest survival rates. Feeding had a greater effect on rates of larval development than did temperature. Although incubation temperature had an overall negligible effect on larval development time, there was a tendency toward fewer instars among larvae that were hatched from eggs incubated at 3°C. Although instar growth rates increased with increasing temperatures, rearing temperatures had no significant effect on final postlarval size. Incubation temperature and feeding level, however, had significant effects on larval growth. Larvae that hatched from eggs that were incubated at 3°C tended to reach larger sizes at metamorphosis at all rearing temperatures and feeding levels. Larvae that were grown on different feeding levels showed significant differences in size at metamorphosis. Experimental results emphasized the differential control of developmental process by temperature and food availability. Fluctuations in temperature prior to larval hatching and in food availability, within and between larval seasons, had profound effects on larval survival, growth, and size at metamorphosis.

CLOSED-SYSTEM PRODUCTION OF SOFT-SHELL BLUE CRABS IN VIRGINIA.

OESTERLING, Michael K.,
Marine Advisory Services, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

Virginia has consistently been a leader in the production of soft-shell blue crabs. For the period 1978-1982, the average production of soft crabs exceeded 317,520 kg, valued at over $780,000. Traditionally, this production was achieved using methods little changed from the early beginnings of the industry. Recently, a great deal of interest has been expressed regarding the shedding of crabs in closed, recirculating water systems. The most prevalent closed system in Virginia includes a biological filter and foam fractionation unit. During the 1982 soft-crab season a direct production comparison between an open, flow-through and a closed, recirculating system within a single facility was conducted. The closed system had a better shedding success for "rank" crabs (those closest to molting) than did the open system (65 and 55.4%, respectively). Similarily, "green" crabs (those farthest from molting held in the closed system had a lower death rate (24 crabs · day^{-1}) than those in the open system (41.1 crabs · day^{-1}). Observations were also made on ammonia and nitrite/nitrate concentrations, water flow rates, dissolved oxygen, and temperature.

EXPLORATORY FISHING FOR DEEP-SEA CRABS (*GERYON*) IN THE GULF OF MEXICO

OTWELL, W. Steven,
SWEAT, Donald E.,
BELLAIRS, Jeffrey J.,
Department of Food Science and Human Nutrition, University of Florida, Gainesville, Florida 32611.

Data from three cruises suggest that bottom longlines with traps can be used to harvest deep-sea crabs (*Geryon* sp.) from the Gulf of Mexico. Five basic trap designs were studied using variable sizes, shapes, entrances, and baits. Trap performance as measured by total catch and sex ratio was influenced by depth and soaktime. Mean crab size was not significantly different across all trap designs,

depths, and soaktimes. Mean body weight for males and females was 1.09 kg (2.4 lb) and 0.45 kg (1.0 lb), respectively. Onboard handling procedures indicated that live storage was impractical. Butchered males yielded 23% total meat when the body parts were steamed and picked. A sodium bisulfite dip and/or thermal processing was necessary to control a black discoloration (melanosis), probably caused by a polyphenol oxidase enzyme system.

SELECTIVE BREEDING FOR IMPROVED MEAT QUALITY IN THE PACIFIC OYSTER *CRASSOSTREA GIGAS* (THUNBERG) IN WASHINGTON STATE.

PERDUE, James A.,
BEATTIE, H.,
HERSHBERGER, W.,
CHEW, K.,
School of Fisheries, University of Washington, Seattle, Washington 98195.

The University of Washington has conducted a selective breeding program with the Pacific oyster *Crassostrea gigas* since 1976. In 1979, one experimental F_2 generation was found which exhibited significantly less gonadal development during the early summer months. The carbohydrate content of this experimental group was consistently higher than any of the other groups monitored during the summer of 1979. In an effort to determine if this trait of reduced gonadal development and increased carbohydrate content could be selected for in our breeding program, this experimental group was crossed with three other groups in a rotational line-crossing design in 1980. In 1982, the 2-year-old progeny (F_3) were monitored for gonadal development, carbohydrate content, and growth. Early gonadal develpment was significantly reduced and the resulting carbohydrate content significantly increased in those groups bred from the high carbohydrate broodstock. Implications of these results on the development of a "summer oyster" stock are discussed.

NUTRITIONAL VALUE OF THREE SPECIES OF ALGAE TO LARVAE OF THE QUEEN CONCH STROMBUS GIGAS (LINNÉ).

PILLSBURY, K.,
Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149.

A series of feeding experiments has shown the relative food value of 3 species of phytoplankton to larvae of *Strombus gigas*. Unialgal diets consisting of the *Isochrysis* aff. *galbana* Parke (clone T-*Iso.*), *Exuviaella* sp., and *Dunaliella tertiolecta* were fed to conch larvae. Larval growth was measured as increase in siphonal length. In every experiment, larvae that were fed the T-*Iso* grew faster than larvae fed any other unialgal diet. In one experiment larvae achieved a length of 800 μm in 13 days when fed the T-*Iso*, while larvae fed *Exuviaella* took 22 days, and larvae that were fed *D. tertiolecta* took 25 days to achieve the same siphonal length.

Biochemical analysis of these species of algae indicated definite differences between protein:lipid:carbohydrate ratios of the 3 species. These differences could be directly related to food value of the algae to conch larvae. Specifically, in the species that supported the fastest growth, the lipid content of T-*Iso* was 20% of the cell while the mean lipid content of 6 other species was 10%. This suggested that the overall composition of phytoplankton was an important factor in determining its nutritive value to the larvae of *S. gigas*.

THE U.S. SHRIMP IMPORT MARKET; LEGISLATION AND IMPACTS ON FISHERY MANAGMENT.

PROCHASKA, Fred J.,
KEITHLY, Walter,
Department of Food and Resource Economics, University of Florida, Gainesville, Florida 32611.

Fishery management may be accomplished in a variety of ways. Management most often is aimed directly at the resource or through management of the users of the resource. Another avenue for management is through legislation affecting transactions in the market place with measures such as tariffs and quotas. This is especially true in the U.S. shrimp industry where nearly one-half of the market originates from shrimp imports. A lack of effective, direct management measures often result in a desire for indirect measures such as tariff and quotas. These measures may affect existing management measures by influencing effort, entry, and exit in the fishery. In this paper, models are developed to analyze the U.S. demand for shrimp imports and the foreign supply of shrimp offered to U.S. buyers. Proposed tariffs and quotas are analyzed with respect to import and export prices, volume and value of imports, incidence of taxation, tax collections, potential profits, and expenditures in the import market. The impacts are extended to the dockside markets to estimate ex-vessel price and production impacts. Finally, the question of further induced entry into the fishery is examined as consequence of tariff and/or quota legislation.

OPTIMUM ALGAL CONCENTRATIONS AND ALGAL CONSUMPTION RATES FOR BIVALVE LARVAE IN CULTURE, AND SOME IMPLICATIONS FOR FEEDING PROTOCOLS.

RHODES, Edwin W.,
WIDMAN, James C., and
GRINBERGS, Elizabeth L.,
National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460.

In two separate types of experiments with larvae of the northern quahog clam *Mercenaria mercenaria* (Linne') and the northern bay scallop *Argopecten irradians irradians* (Lamarck), the optimum concentrations of *Isochrysis* aff. *galbana* Parke (clone T-*Iso*) for growth were determined, and estimates made of the algal consumption rates. In the concentration experiments, larvae of these species were grown for the entire larval period in static culture at extremely low densities so that the *Isochrysis* concentrations remained constant. Algal consumption rates for larvae of different sizes were determined in a series of short-term tests in which fluorometric techniques were used to monitor the loss of *Isochrysis* cells from culture containers, and to allow rapid refeeding of cultures to maintain approximately constant algal concentrations. The synthesis of the optimum algal concentration data and the larval consumption rates presents a clear picture of the larvae-food interactions in culture systems, and suggests some new feeding strategies for experimental and commerical aquaculture.

STATUS OF GEOTHERMAL AQUACULTURE IN THE UNITED STATES.

RHODES, Raymond J.,
SMITH, Theodore J.,
TAYLOR, Frank S.,
South Carolina Division of Marine Resources, Charleston, South Carolina 29412.

Identified low-temperature (< 90°C) geothermal systems in the United States contain an estimated beneficial heat of 36.9 x 10^{15} J (35 x 10^{15} Btu [35 Quads]). These systems are separated into conduction-dominated systems and hydrothermal convection systems. Substantial research has been conducted on the utilization of thermal effluents from power generating stations for aquaculture; however, only limited information is available on efforts to develop extensive geothermal water resources for aquatic food production in the U.S. There are several firms in the Western states using geothermal well water to commerically produce the channel catfish *Ictalurus punctatus* (Rafinesque). Additionally, some private research and development projects are examining the application of geothermal water for the culture of various warm water species including *Tilapia* and ornamental species. The freshwater prawn *Macrobrachium rosenbergii* de Man is a target species for a number of geothermal aquaculture research and development projects in California, Nevada, South Carolina, and Texas. Current geothermal aquaculture technology involves the direct use of hydrothermal well water as a culturing medium. Wells at most sites are < 400 m deep with flow rates in the range of 190 to 28,400 $L \cdot min^{-1}$. Water temperatures are usually less than 55°C. The use of geothermal water by aquaculture firms offers a number of advantages including reduced heating and pumping costs, expansion of suitable farming sites for both indigenous and nonindigenous species, and development of local specialty markets.

INTERTIDAL PATTERNS OF DISTRIBUTION IN THE SOFT-SHELL CLAM *MYA ARENARIA* (LINNÉ) ON A NEW JERSEY TIDAL FLAT.

SCAPATI, Dominick Jr.,
Department of Biological Sciences, Rutgers University, Nelson Biological Laboratory, P.O. Box 1059, Piscataway, New Jersey, 08854.

A 2-year study initiated in the winter of 1981 analyzed the patterns of distribution in a population of *Mya arenaria* on an intertidal flat off Shark River Island, Belmar, NJ. Adult clams were aggregated as a dense band below the lower boundary of a stand of *Spartina alterniflora* Loisel and above mean tide level. This was in direct contrast to the nonaggregate pattern seen in the setting of the 1981- and 1982-year classes. Substrate, wave action, and predation were investigated in an attempt to explain why previous year classes were seldom found below mean tidal level. The absence of any similarity between the patterns of clam and sediment distribution, and insufficient wave action indicates that these factors are not responsible for the aggregate pattern that appeared the 2nd week of August, approximately 8 wk after the set of the new year classes. An exclosure experiment suggested that marine predators, notably several crab species and naticid snails, could account for the transformation of a population from a nonaggregate distribution of postlarval clams to a strongly aggregated, upshore remnant of the older year classes. The transformation corresponded to a peak and subsequent decline in the number of predators present on the flat.

GEORGIA SOUNDS: AN EVALUATION OF SHRIMP MANAGEMENT STRATEGY.

SHIPMAN, Susan,
ESSIG, Ronald J.,
Georgia Department of Natural Resources, Coastal Resources Division, Brunswick, Georgia 31523.

The management strategy of inshore areal closure to commerical shrimp trawling was effected in 1977 by the Georgia Department of Natural Resources to protect the few remaining spawners following decimation of the over-wintering white shrimp stocks in 1977. Mean 1977 fall production, characterized by larger, high-value shrimp, and coupled with a successive 1978 winter kill of inshore shrimp stocks prompted a continuation of the closure of the sounds. Analyses of inshore shrimp sizes and count sizes of commerical fall production prior to and following 1977 indicated factors in addition to the management strategy that were as important in the determination of the size of shrimp at emigration from the sounds. Commercial landings data and mark-and-recapture results revealed that sound closures during periods of environmental extremes such as fall 1980 effected less than optimum harvest. Biological and socio-economic implications of alternate management strategies are discussed with respect to the shrimp resource, other resources, and resource users.

APPLICATION OF GEOTHERMAL RESOURCES FOR PRAWN AQUACULTURE IN SOUTH CAROLINA.

SMITH, Theodore I.J., and
WANNAMAKER, Allen J.,
Marine Resources Research Institute, P.O. Box 12559, Charleston, South Carolina 29412.

Research was conducted to assess the potential application of geothermal water resources for culturing the freshwater prawn *Macrobrachium rosenbergii* de Man. In coastal South Carolina, 23 existing well sites were identified. Well depth averaged ~615 m and temperature averaged ~37°C. Artesian flow rates varied from 190 to 2,650 $L \cdot min^{-1}$. In general, the geothermal waters were higher in chlorides, fluorides, dissolved solids, pH, alkalinity, and ammonia levels as compared to surface waters. A short-term replicated laboratory study was conducted to examine the effect of geothermal water on survival of small juvenile prawns. After 42 days, very low survival rates were recorded from the various 100% geothermal water treatments. A 1:1 mixture of shallow well water and geothermal water, however, resulted in a survival rate of 83%, which was similar to that observed among the control animals. Next, a large-scale study was initiated at a local site which had both shallow well water (control) and geothermal water available. Treatments consisted of various dilution rates for the geothermal water. After 12 weeks, the survival rate was 88% in the control tank as compared to 6% in the 100% geothermal, 73% in the 75% geothermal, and 85% in the 50% geothermal water treatments. Thus, at least on a shrot-term basis, a dilution rate of 25 to 50% appears satisfactory. Longer term biological studies and economic analyses will be needed to properly assess the aquaculture potential of utilizing geothermal water to rear freshwater prawns in South Carolina.

SEASONAL CHANGES IN LEVELS OF PARASITISM OF *PERKINSUS MARINUS* (MACKIN, OWEN, AND COLLIER) IN *CRASSOSTREA VIRGINICA* (GMELIN), WITH SPECIAL REFERENCE TO THE LIMITED ASSOCIATION BETWEEN PARASITISM AND TEMPERATURE AND SALINITY.

SONIAT, Thomas M.,
Department of Biological Sciences, University of New Orleans, Lakefront, New Orleans, Louisiana 70148.

Twenty-six monthly samples of oysters were collected from Galveston Bay, Texas, from May 1979 to September 1981. The level of parasitism of *Perkinsus marinus* was determined in 520 oysters. Percent infection and weighted incidence (WI) of *P. marinus* were calculated for each monthly sample and factors known to be related to parasitism were measured (oyster length [L], and water temperature [T] and salinity [S]). An analysis of variance of parasitism by month indicated that the variability of parasitism within a monthly sample was significantly less than the variation between samples. Duncan's multiple-range test was used to define groups of samples among which there were no significant differences in WI. Highest and lowest values of WI were found during months representing every season of the year. Correlations between WI and I ($r = 0.14$) and WI and L ($r = 0.38$) were not significant (all tests of significance were made at the $\alpha = 0.05$ level). A correlation between WI and S was significant ($r = 0.51$). Elevated levels of parasitism are known to be associated with high temperature and high salinity. Some summer samples, however, had the lowest WI values recorded, although they were always coupled with salinities below 10 $^{o}/_{oo}$. Likewise, some winter samples (at $S > 15\,^{o}/_{oo}$) had high values of WI. A significant inverse correlation ($r = 0.42$) between T and S was found. An interaction factor (defined as the product of T and S) was significantly correlated with WI ($r = 0.70$). Thus, the product of T and S is more closely related to WI than is T or S alone; however, only about 49% of the variability in WI is explained by the TxS interaction. Genetically determined resistance to disease is likely a major source of the unexplained variation.

DEVELOPMENT OF FIELD GROWOUT TECHNIQUES FOR THE NORTHERN HARD-SHELL CLAM *MERCENARIA MERCENARIA* (LINNÉ) IN SOUTH CAROLINA

STEVENS, Fred S.,
MANZI, J. J.,
Marine Resources Research Institute, Charleston, South Carolina 29412;
CLAWSON, H. Q. M.,
Trident Seafarms Co., Charleston, South Carolina 29401.

The Marine Resources Research Institute/Trident Seafarms Company cooperative hard-shell clams mariculture project utilizes a 2-phase intertidal growout procedure in the commercial production of marketable (45-50 mm) clams. Nursery-reared seed clams (~ 8 mm) were planted in primary field units at a density of 8800 m^{-2}. As the seed attained a size of 20 to 25 mm (9 to 12 months) they were thinned into secondary field units at a density of ~ 1100 m^{-2}. The design of both primary and secondary field units has changed considerably over the 3-year project. Retrieval of clams from primary and secondary field units is accomplished by hydraulicly lifting units from a specially designed barge or directly harvesting clams from submerged units by venturi suction. Field planting of nursery-reared seed through the cooperative project has increased from 600,000 seed in 1980 to 2.4 and 2.9 million seed in 1981 and 1982, respectively. Field plants for 1983 are projected to exceed 12 million seed. Harvest size (45-50 mm) clams were retrieved from initial plants in November 1982, exactly 24 months from first primary unit deployment. Mean recovery from secondary field units harvested to date was 79% and overall field survival was over 50%. This paper traces the evolution of field unit design and operational procedures over the first 3 yr of the cooperative project, discusses problems associated with field growout of hard-shell clams in South Carolina, and summarizes results of field operations to date.

NATURAL FOOD SOURCE IN OYSTERS IN GEORGIA.

STEVENS, Stuart A.,
Department of Natural Resources, Brunswick, Georgia 31523.

Four criteria that are necessary to demonstrate the nutritive role of a substance are discussed in relation to bacteria and detritus. The major components of detritus, *Spartina* and bacteria, were investigated separately. Both substances satisfied the criteria although ^{14}C-labeling experiments indicated that detritus may be a substrate for microbiota rather than a food source itself. Detritus, however, was the most abundant food source. Experiments using ^{14}C-labelled bacteria clearly showed that *Crassostrea virginica* (Gmelin) assimilated ^{14}C orginating from the bacteria. Although other materials such as dissolved organic moleculas and suspended benthic diatoms were possible foods of the oyster, aged detritus enriched with bacteria probably makes up the bulk of the oyster's diet.

ASPECTS OF COLORIMETRIC STEROL ANALYSIS ON MOLLUSCAN SAMPLES.

SWIFT, M. L.,
Department of Biochemistry College of Medicine, Howard University, Washington, DC 20059.

The simplicity, efficiency, and inexpensiveness of colorimetric sterol methods help to maintain their popularity; however, difficulties associated with colorimetric (chole) sterol analysis on extracts of bivalve molluscs have been recognized since 1937. These problems may be traced directly to the diverse spectra of sterols normally found in these animals. A series of oyster (*Crassostrea virginica* [Gmelin]) samples were analyzed using three colorimetric procedures. The methods employed were a modified Liebermann-Burchard reaction, an $FeCl_3/H_3PO_4/H_2SO_4$ reagent, and colorimetric cholesterol oxidase. On average, values of total sterol content obtained by the $FeCl_3/H_3PO_4/H_2SO_4$ and cholesterol oxidase procedures were 36% and 29%, respectively, higher than those obtained using the Liebermann-Burchard method. The $FeCl_3/H_3PO_4/H_2SO_4$ and cholesterol oxidase values agreed to within 5.4% on average. Several pure sterols, selected because of their presence in molluscan sterol fractions or because of their structural similarities to such sterols, were examined using each of the three procedures. On a molar basis, sterols differing from cholesterol only with regard to side chain substitution, reacted 80-102% as well as cholesterol with the $FeCl_3/H_3PO_4/H_2SO_4$ reagent and cholesterol oxidase. The Liebermann-Burchard reaction was more specific for cholesterol. The colorimetric cholesterol oxidase method is recommended for use in the estimation of total molluscan sterol content.

INDUCED TRIPLOIDY IN THE ATLANTIC BAY SCALLOP *ARGOPECTEN IRRADIANS* AND ITS EFFECT ON GROWTH AND GAMETOGENESIS.

TABARINI, C. L.,
Oceanography Program, Ira C. Darling Center, University of Maine, Walpole, Maine 04573.

Triploidy was induced in the Atlantic bay scallop *Argopecten irradians* (Lamarck) by treating newly fertilized eggs with

cytochalasin B. In treatments beginning 10 min after fertilization and lasting 10 min, 66% of scallops treated with 0.05 mg·L^{-1} cytochalasin were triploid and 94% of scallops treated with 0.1 mg·L^{-1} cytochalasin were triploid. In yearling triploid scallops, significant increases were found in shell inflation, adductor muscle weight, and glycogen level, whereas gonadal development was retarded. Other parameters, such as shell height and length, were unaffected. These differences are discussed in terms of physiological mechanisms and the relevance they hold for mariculture.

PRELIMINARY ANALYSIS OF THE EFFECT OF A COMMERCIAL FISHERY ON THE SIZE STRUCTURE OF POPULATIONS OF THE SNOW CRAB *CHIONOECETES OPILIO* (FABRICIUS) IN SEVERAL NEWFOUNDLAND AREAS.

TAYLOR, David M.,
Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1.

Snow crabs (*Chionoecetes opilio*) have been fished commercially in Newfoundland since 1968. Fishing effort and landings have increased dramatically since inception of the fishery with exploitation rates in some areas reaching 70% and higher. To date, little effort has been expended to determine what effect commerical exploitation has on size structure and shell condition of adult snow crabs. Data on carapace width of crabs caught during pre-exploitation surveys are compared to data obtained from the recent commerical fishery to determine what effect fishing on a commerical level has on size frequency distribution.

RECENT ADVANCES IN OCTOPOD SYSTEMATICS AND THEIR BEARING ON FISHERY DEVELOPMENT.

TOLL, Ronald B.,
Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.

The commercial exploitation of octopuses as part of the United States fishery effort is in its formative stages. The Octopodidae, which includes the benthic, littoral species of octopuses, is recognized as one of the four most important families of cephalopods in terms of world-wide fishery potential. It is also one of the most in need of comprehensive, systematic revision. The lack of a clearer understanding of the biology and systematics of these animals stands as a major impediment to future, increased levels of exploitation. Such problems have been documented from the octopus fishery in the Bay of Campeche where an undescribed species supported the fishery. Similar examples are known in relation to other exploited species. Present study on intra- and interspecific variation has demonstrated a need for revisionary work at the generic and specific levels. Bodily measurements of octopuses are often unsatisfactory for comparing taxa. Characters under present study include aspects of the male and female reproductive, alimentary, respiratory, and skeletal (shell vestige) systems. Characters are sought that will provide for simple and accurate field identifications by fishermen and fishery scientists. Information gained through these studies can also provide data on life history parameters. Additional study is required to more firmly establish the systematics and biology of the group. Resultant data will be important to future considerations of fishery development and proper fishery management.

A COMPARISON OF FOOD INTAKE, FOOD CONVERSION EFFICIENY, AND GROWTH RATE OF *OCTOPUS CYANEA* GRAY AND *OCTOPUS MYA* VOSS AND SOLIS.

VAN HEUKELEM, William W. F.,
Horn Point Environmental Laboratories, University of Maryland, Cambridge, Maryland 21613.

Growth, feeding rate, and food conversion efficiency of *Octopus cyanea* and *O. maya* were studied in the laboratory. Both species reached similar adult size (>5 kg). Growth rate of *O. maya* was faster than that of *O. cyanea*. No difference in food conversion efficiency was found between the two species. Both species converted about 40% of ingested food (live crabs) into body weight (wet weight). Analysis of data on rate of food intake revealed that *O. maya* ingested a higher percentage of its body weight per day and thus was able to grow faster than *O. cyanea*.

A COMPUTERIZED ACTIVITY MONITOR FOR BLUE CRABS AND OTHER AQUATIC ANIMALS.

VAN HEUKELEM, William F., and SULKIN, S. D.,
Horn Point Environmental Laboratories, University of Maryland, Cambridge, Maryland 21613.

We have designed and built an activity monitor that will simultaneously record activity of 18 individual crabs. The activity

monitor consists of 3 independent units, each with 6 individual compartments. Each compartment houses a crab and is equipped with an infrared LED (Light emitting diode) and sensor to detect movement of the crab. Each of the 3 units has its own circuit board which filters out "noise" and transmits data to a 20-channel event recorder and a microcomputer. The event recorded produces a back-up "hard copy" of raw data while the computer stores data directly on a diskette. Data analysis, using a modification of the Enright Periodogram, is performed by the microcomputer. Preliminary results of the effects of photoperiod and substratum on crab activity rhythms will be presented.

GROWTH RATE OF A SINGLE YEAR CLASS OF THE ATLANTIC SURF CLAM *SPISULA SOLIDISSIMA* (DILLWYN) OFF ATLANTIC CITY, NEW JERSEY.

WAGNER, Eric S.,
Department of Oyster Culture, NJAES, Cook College, Rutgers University, New Brunswick, New Jersey 08903.

Length-frequency and shell-structure analyses of a predominantly single year class of surf clams (*Spisula solidissima*) have revealed a relationship between shell growth and distance from shore (depth). Results confirmed the formation of one translucent growth band (when viewed in polished thin section) per year. While supporting the conclusion of Jones (1980), this study also showed that growth rate can be inversely proportional to population density and that timing of band formation and relative width of bands were related to distance from shore. Since 1979, growth of the 1976 year-class of surf clams off Atlantic City, NJ, was monitored by repeated sampling of stations lying on transects normal to the coast and extending 0.9 to 22.2 km (0.5 to 12 mi) offshore. Surface and bottom temperatures, population density, sediment type, and gonad condition were determined at each station. In general, clams located further offshore grew faster. After 6 years, offshore clams were as much as 45 mm longer than inshore clams of the same age. At stations equidistant from shore but differing in density, clams were significantly ($p < 0.01$) longer in less densely populated areas. Clams, from a very densely populated offshore station, however, were shorter than inshore clams in less densely populated areas. Translucent band formation persisted over several months, beginning as early as May and continuing into December in some years. Translucent bands appear to form when bottom temperatures are between 10.5 and 20.8°C. No relationship between band formation and gametogenic stage was apparent.

OBSERVATIONS OF THE POPULATION OF THE STONE CRAB *MENIPPE MERCENARIA* (SAY) IN WATERS NEAR CHARLESTON, SOUTH CAROLINA.

WENNER, Elizabeth L.,
STOKES, A. D.,
Marine Resources Research Institute, Charleston, South Carolina 29412.

Collections of stone crabs were made at 7 locations near Charleston, SC, from July to September 1982. In each location sampled, 5 commercial, wire blue crab traps with two entrance holes and 5 wooden-lath stone crab traps, similar to those used in the Florida fishery, were fished for 2 and 3 days in paired sets. Twice as many stone crabs were collected in the blue crab trap as in the stone crab trap, and for 6 of the sites sampled, catches in the blue crab trap were significantly greater than those in the stone crab trap. No significant differences were found in the number of crabs per trap between 2-day and 3-day sets of either trap type. The cumulative number of stone crabs per trap did not noticeably decline over the period of study; however, the net increase in catch for the duration of sampling appeared to be greater for the blue crab trap. Data collected on sexual maturity, sex ratios, carapace width frequency, and handedness are presented and compared to similar information from the Florida fishery.

EFFECT OF SEVERE WINTER WEATHER ON WHITE SHRIMP STOCKS IN THE ATLANTIC OCEAN OFF THE SOUTHEASTERN UNITED STATES

WHITAKER, J. David
South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina 29412.

The white shrimp *Penaeus setiferus* (Linnaeus) is the most important species in the South Atlantic Bight shrimp fishery which is the most valuable fishery in the region. The relative abundance of white shrimp, along the Atlantic coast as reflected by commercial landings, indicates that the species increases in abundance with decreasing latitude. Severe winters have periodically caused large fluctuations in landings, particularly in the Carolinas and along the northern Georgia coast. In South Carolina, shrimp mortalities apparently begin to occur as water temperature approaches 6°C. The winter's effect on the shrimp population appears to be related to duration of cold temperatures, lowest temperature, and salinity. The lowest landings since 1950 have followed the severe winters of 1963 and 1977, while above average landings have followed mild winters. Subadult white shrimp, 80-110 mm total length, remain in the

estuarine and nearshore waters during mild winters and make up the bulk of the spring spawning population. When severe winters cause mass mortalities of overwintering shrimp, the Carolinas are dependent on spawning by large shrimp that migrate north from the warmer waters of southern Georgia and northeastern Florida. The progeny of the spring spawn reach marketable size by late August and are fished during the "fall" season (August-December). The fall white shrimp season contributes the greatest share of the region's shrimp landings. A very poor spring spawn can result in low fall landings and larger than normal shrimp.

Journal of Shellfish Research, Vol. 4, No. 1, 105—111, 1984

ABSTRACTS OF TECHNICAL PAPERS

Presented at the 37th Annual Convention of the Pacific Coast Oyster Growers Association and the Pacific Coast section of the National Shellfisheries Association

NATIONAL SHELLFISHERIES ASSOCIATION

Tumwater, Washington

September 9 — 10, 1983

CONTENTS

STUDIES OF JUVENILES OF THE DUNGENESS CRAB *CANCER MAGISTER DANA* IN GRAYS HARBOR, WASHINGTON

ARMSTRONG, David A., D. R. GUNDERSON, K. R. CARRASCO, and C. RODGERS.
School of Fisheries, University of Washington, Seattle, Washington 98195.

A progress report is presented on an ongoing 2-year project evaluating the significance of Grays Harbor, WA, as a nursery ground for local Dungeness crab populations. Some preliminary findings are presented, but the sampling design and technical aspects of the project which have been refined are emphasized. The latter include the reasons for selection of the plumb-staff beam trawl over the otter trawl, design of the trawl gear on both the skiff that was used within the Harbor and the 55-ft salmon charter boat that was used for a comparative offshore survey, methods of documenting trawl positions within the Harbor without electronics, and determination of distance towed.

INCREASED SURVIVAL AMONG PACIFIC OYSTERS: THE RESULT OF SELECTIVE BREEDING.

BEATTLE, J. Harold,
College of Oceanography and Fisheries Science, university of Washington, Seattle, Washington 98195.

Second generation (F_2) groups of oysters (progeny of single male and female mating) were selected for the breeding season of 1980. Three groups were chosen on the basis of low mortality rate during the summer of 1979 (one from each of three bays). Mortality rates were: Mud Bay, 23.6% compared to nonselected control at 56.1%; Oakland Bay, 11.3% compared to 56.6% for control; Rocky Bay, 23.0% compared to 35.2% control. In addition, one group was chosen for breeding on the basis of high glycogen content. The four groups were crossed using a rotational line scheme. All offspring (F_3) groups were planted in 1981 and monitored for mortality during the summer of 1982. The lowest mortality group in Mud Bay was derived from parents that were selected from Mud Bay and crossed with high glycogen parents. Mortality was 12.3% compared to 62.4% for controls. The lowest mortality groups in Oakland and Rocky bays were derived from crosses of parents selected from those respective bays. Mortalities were: Oakland Bay, 6.9% compared to 34.2% for controls; Rocky Bay, 10.0% compared to 23.3% for controls. The results indicated a difference between bays with regard to survival potential of selected stocks during summer mortality. As a consequence, breeding for increased survival may need to be tailored to individual bays.

PRELIMINARY REPORT ON DEEPWATER CULTURE OF *CRASSOSTREA GIGAS* THUNBERG AT SEVEN SITES IN BRITISH COLUMBIA

COX, Robert K.,
Shellfish Management and Development Section, Marine Resources Branch, Ministry of Environment, Parliament Buildings, Victoria, British Columbia, Canada, V8V 1X5.

Seven coastal sites in British Columbia were assessed for deepwater culture of the Pacific oyster *Crassostrea gigas* using a variety of hanging culture techniques. Seed oysters from the 1980 Pendrell Sound set (mean shell length = 8 mm) were suspended at experimental sites from February to July 1981. Additional oysters were suspended at one site in October 1981 using beach-hardened, 1980 Pendrell oysters. A total of 14,000 grow-out strings were placed at the 7 sites. Shell growth, fouling, condition index, temperature, and salinity were monitored from July 1981 to August 1983. Shell growth averaged 60 mm in 1981 and 30 mm in 1982. Shell length at harvest averaged 108 mm. Condition indexes at all sites were high in mature oysters and generally higher than values reported for bottom-cultured oysters. Condition indexes showed large variations. The blue mussel *Mytilus edulis* Linne' was the predominant fouling organism at all sites. A further 45 species of fouling organisms were identified. Fouling increased floatation requirements significantly at some sites and reduced growth rate.

BIOASSAY DEVELOPMENT FOR THE JAPANESE OYSTER DRILL *OCENEBRA INORNATA* (RÉCLUZ)

CURREN, E. Flinn,
School of Fisheries, University of Washington, Seattle, Washington 98195

Two bioassays were developed to test the chemotatic behavior of adults of Japanese oyster drill *Ocenebra inornata*. The dynamic-water bioassay tested the reaction of snails in a divided flume with 500 ml·min^{-1} flowing across each side. The static-water bioassay presented the same types of seawater to individual snails placed in large culture tubes. In both bioassays the snails were presented with either aged seawater or aged seawater with 10% stimulus (aged seawater in which seed oysters had rested for 24 h and which was sterile filtered and frozen until use). In the flame, snail response was considered positive if the snail moved 5 cm beyond the starting area. Significant response (as tested by the G-statistic) 1 h after exposure to 10% stimulus was noted when snail numbers of 20 or less were placed in each 500 cm^2 area; at higher snail densities many snails became attached to each others' shells. Snail

response in the static bioassay was based on observations of changes in the snails' locations in the tubes initially and at 15-min intervals. Initial position was estimated by the distance from the bottom of the tube to the lowest portion of the shell aperture. Following attachment of the snail's foot, position was determined by the distance from the lowest portion of each foot to the bottom of the tube. Snails that failed to attach their foot at the end of 30 min were excluded from statistical analysis by the T-test. Significant response to 10%-stimulus water was noted despite large variations in individual response. The static water was noted by the test snails despite large variations in individual responses. The static-water bioassay used less stimulus water and eliminated snail-to-snail interactions during each test. Absorption and subsequent release of stimulus onto snail shells may have affected the result of both bioassays.

PATHOLOGY AND CERTIFICATION OF THE JAPANESE SCALLOP, *PATINOPECTEN YESSOENSIS*: A CASE HISTORY.

ELSTON, Ralph A.,
Center for Marine Disease Control, Battelle Marine Research Laboratory, Sequim, Washington 98382
BURGE, Richard,
Pt. Whitney Shellfish Laboratory, Washington Department of Fisheries, Brinnon, Washington 98320

Pathological examination in relation to the attempted certification for importation of the Japanese scallop, *Patinopecten yessoensis* (Jay), from Mutsu Bay, Amori Prefecture, into Washington State is reported. The species has been imported into California and into a quarantine facility in British Columbia, Canada. To preliminarily determine if the scallop meets the state's import standards for shellfish seed, a presample was examined for infectious pathogens, parasites, and associated predators. The presample consisted of 8 adults (~ 8 cm, S.H.) and 28 juveniles (~ 3 cm, S.H.). Gross examination revealed an attached, yellow glistening, spheroidal body (~ 3 mm, dia) at the base of the branchial tissue of one juvenile. Histologically, the body was heavily encapsulated, contained apparent ova, and was deeply attached to the gill base by interdigitating fiberous extensions of its tissue. The spheroidal body, according to published accounts, is apparently a parasitic rhizocephalid barnacle, *Sacculina* sp. Infiltrative scallop hemocytes were associated with the parasite. Occasional instances of rickettsia-like prokaryotes were observed in gill tissue in several scallops. Concern about the *Sacculina*-like organism resulted in further evaluation and a determination that the importation of Japanese seed scallops would not be permitted. The presence of these parasites on the seed would probably be a continuing phenomenon; therefore, the culture of F_1 scallops in quarantine facilities is being developed. A pathological examination, including native scallop exposure, will accompany such culture efforts.

THE RELATIONSHIP BETWEEN SUMMER MORTALITY IN CULTURED BLUE MUSSELS *MYTILUS EDULIS* AND THE ANNUAL CYCLING OF ENERGY STORAGE PRODUCTS.

EMMETT, Brian T., and R. L. BADEN,
Archipelago Marine Research, P.O. Box 6418, St. C, Victoria, British Columbia, Canada, V8X 5M3.

Populations of cultured blue mussels at a number of sites in British Columbia and Washington State experience high mortalities of an unknown origin during the second summer of growth. We examined the growth and mortality of test populations of *Mytilus edulis* at two locations on the eastern and western coasts of Vancouver Island over a 1-yr period. Mussels were grown at the surface and at a depth of 5 m in both study locations. Glycogen, lipid, and protein levels in the test populations were measured throughout the year and environmental conditions, such as water temperature, salinity, dissolved oxygen, and chlorophyll were monitored on each sampling date. Cumulative mortalities at both sites exceeded 70% over the summer and fall period. Mussels that were grown at the surface and at 5 m showed no distinct differences in patterns of growth and mortality. The mortalities were not directly correlated with either seasonal water temperature maxima or salinity minima. Glycogen and lipid levels in mussels from both sites revealed a peak of spawning in May and June, and a delay in postspawning recovery of glycogen levels until September. Spatfall from the more sheltered eastern Vancouver Island site indicated a protracted period of spawning from May until November. We believe that this pattern of spawning may have contributed to the observed mortalities.

THE FEASIBILITY OF THE GOOSENECK BARNACLE *LEPAS ANATIFERA* AS A CANDIDATE FOR MARICULTURE.

GOLDBERG, Harry, J. W. ZAHRADNIK,
Department of Bio-Resource Engineering, University of British Columbia, 2357 Main Mall, Vancouver, British Columbia, Canada, V6T 1W5.

The acquisition of seed and the subsequent suspension culture of the gooseneck barnacle *Lepas anatifera* was investigated. *Lepas*

anatifera successfully colonized the cultch (oyster shells, wooden dowelling, and rubber) that was developed at two locations off the western coast of Vancouver Island. Our experiment indicated that growth rate may be site-specific and that areas of a high phytoplankton: zooplankton ratio may be a detriment to growth and timing of sexual maturation. At the densities studied, survival appeared to be proportional to density. Capitulum growth and weight gain were significantly greater for barnacles that were protected from predation within lantern nets than for those grown exposed on lines of oyster shells and wood dowelling. The mean total growth (capitulum plus peduncle) exceeded 4 cm in length within 17 to 23 weeks.

RECENT PROGRESS IN PARALYTIC SHELLFISH POISONING RESEARCH

NISHITANI, Louisa, Kenneth K. CHEW,
School of Fisheries, University of Washington, Seattle, Washington 98195.

Marked increases in the percent of cells of *Gonyaulax catenella* that were infested by an endoparasitic dinoflagellate, *Amoebophrya ceratii* have been associated with the decline of two blooms of *G. catenella* in Quartermaster Harbor. In each of those blooms the nitrate concentrations declined prior to or with the decline in the population of *G. catenella* and prior to the major rise in the rate of parasitism. This suggested that infestation of *G. catenella* by *A. ceratii* may be easier in nutrient-stressed host cells. The high number of infestive spores that are produced by *A. ceratii* in each host cell and the relatively high host specificity (observed in only 4 other species in Quartermaster Harbor) are characteristics of *A. ceratii* which suggested it may be useful as a biological control agent in certain confined bays. Additional extensive laboratory testing is required to evaluate the acceptability and feasibility of using this form of control.

SELECTIVE BREEDING FOR IMPROVED MEAT QUALITY IN THE PACIFIC OYSTER *CRASSOSTREA GIGAS* IN WASHINGTON STATE

PERDUE, James A., H. BEATTIE W. HERSHBERGER, and Kenneth K. CHEW,
School of Fisheries, University of Washington, Seattle, Washington 98195.

The University of Washington has conducted a selective breeding program with the Pacific oyster *Crassostrea gigas* since 1976. In 1979, one F_2 experimental group was found which exhibited significantly less gonadal development during the early summer months. The carbohydrate content of that experimental group was consistently 50% higher than any of the other groups monitored during the summer of 1979. In an effort to determine if this trait of reduced gonadal development and increased carbohydrate content could be selected for in our breeding program, that experimental group was crossed with three other groups in a rotational, line-crossing design in 1980. In 1982, the 2-year-old progeny (F_3) were monitored for gonadal development, carbohydrate content, and growth. Early gonadal development was significantly reduced and the resulting carbohydrate content significantly increased in those groups that were bred from the high carbohydrate broodstock.

LIPID REQUIREMENTS FOR LARVAE OF *STROMBUS GIGAS* (LINNÉ)

PILLSBURY, K.
Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149.

The nutritional value of 6 phytoplankton species to larvae of *Strombus gigas* were compared. A large difference in growth rate of queen conch larvae was dependent on the phytoplankton diet. Biochemical analysis of phytoplankton diets showed a positive correlation between food value and lipid content of the algae. Next, lipid content was modified artificially within phytoplankton species. It was found that increasing the lipid content of phytoplankton species with a below average lipid content caused an increase in food value. Conversely, increasing the lipid content of an algal species which normally has a high lipid content caused a decrease in food value. It was determined that a lipid content of approximately 15% in the phytoplankton diet is optimum for larval conchs.

AGE AND GROWTH OF THE PACIFIC WEATHERVANE SCALLOP *PATINOPECTEN CAURINUS* OFF OREGON

STARR, Richard M., Jean E. McCRAE,
Oregon Department of Fish and Wildlife, Newport, Oregon 97365.

Scallop surveys conducted in 1981 revealed age and growth differences between scallops off Coos Bay and Tillamook Head, OR. One strong year-class dominated the Coos Bay beds, whereas several year-classes were well represented off Tillamook Head. Scallop growth rates were greater off Coos Bay than off Tillamook Head, and greater in shallower water. Although growth rates differed, scallop weight-to-height ratios were similar in both areas. Analysis of shell annuli height revealed a positive Lee's phenomenon in both scallop beds. No evidence of scallop migration was observed.

INFORMATION FOR CONTRIBUTORS TO THE *JOURNAL OF SHELLFISH RESEARCH*

Original papers dealing with all aspects of shellfish research will be considered for publication. Manuscripts will be judged by the editors or other competent reviewers, or both, on the basis of originality, content, merit, clarity of presentation, and interpretations. Each paper should be carefully prepared in the style followed in Volume 3, Number 1, of the *Journal of Shellfish Research* (1983) before submission to the Editor. Papers published or to be published in other journals are not acceptable.

Title, Short Title, Key Words, and Abstract: The title of the paper should be kept as short as possible. Please include a "short running title" of not more than 48 characters including space between words, and approximately seven (7) key words or less. Each manuscript must be accompanied by a concise, informative abstract, giving the main results of the research reported. The abstract will be published at the beginning of the paper. No separate summary should be included.

Text: Manuscripts must be typed double-spaced throughout one side of the paper, leaving ample margins, with the pages numbered consecutively. Scientific names of species should be underlined and, when first mentioned in the text, should be followed by the authority.

Abbreviations, Style, Numbers: Authors should follow the style recommended by the fourth edition (1978) of the *Council of Biology Editors [CBE] Style Manual*, distributed by the American Institute of Biological Sciences. All linear measurements, weights, and volumes should be given in metric units.

Tables: Tables, numbered in Arabic, should be on separate pages with a concise title at the top.

Illustrations: Line drawing should be in black ink and planned so that important details will be clear after reduction to page size or less. No drawing should be so large that it must be reduced to less than one third of its original size. Photographs and line drawings preferably should be prepared so they can be reduced to a size no greater than 17.3 cm X 22.7 cm, and should be planned either to occupy the full width of 17.3 cm or the width of one column, 8.4 cm. Photographs should be glossy with good contrast and should be prepared so they can be reproduced without reduction. Originals of graphic materials (i.e., line drawings) are preferred and will be returned to the author. Each illustration should have the author's name, short paper title, and figure number on the back. Figure legends should be typed on separate sheets and numbered in Arabic.

No color illustrations will be accepted unless the author is prepared to cover the cost of associated reproduction and printing.

References Cited: References should be listed alphabetically at the end of the paper. Abbreviations in this section should be those recommended in the *American Standard for Periodical Title Abbreviations*, available through the American National Standards Institute, 1430 Broadway, New York, NY 10018. For appropriate citation format, see examples at the end of papers in Volume 3, Number 1, of the *Journal of Shellfish Research* or refer to Chapter 3, pages 51—60 of the *CBE Style Manual*.

Page Charges: Authors or their institutions will be charged $25.00 per printed page. If illustrations and/or tables make up more than one third of the total number of pages, there will be a charge of $30.00 for each page of this material (calculated on the actual amount of page space taken up), regardless of the total length of the article. All page charges are subject to change without notice.

Proofs: Page proofs are sent to the corresponding author and must be corrected and returned within seven days. Alterations other than corrections of printer's errors may be charged to the author(s).

Reprints: Reprints of published papers are available at cost to the authors. Information regarding ordering reprints will be available from the National Shellfisheries Association at the time of printing.

Cover Photographs: Particularly appropriate photographs may be submitted for consideration for use on the cover of the *Journal of Shellfish Research*. Black and white photographs, if utilized, are printed at no cost. Color illustrations may be submitted but all costs associated with reproduction and printing of such illustrations must be covered by the submitter.

Corresponding: An original and two copies of each manuscript submitted for publication consideration should be sent to the Editor, Dr. Roger Mann, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

JOURNAL OF SHELLFISH RESEARCH

Vol. 4, No. 1 June 1984

CONTENTS

COVER PHOTOMICROGRAPH: Scanning electron micrograph of a juvenile queen conch (*Strombus gigas* Linné) 45 days after hatching (4-mm siphonal length). Note distinct change in pattern of shell growth lines at the protoconch II/teleoconch boundary which occurs at metamorphosis. [Photograph provided by Scott Siddall, State University of New York, Stony Brook, New York.]

JOURNAL OF SHELLFISH RESEARCH

VOLUME 4, NUMBER 2 DECEMBER 1984

The *Journal of Shellfish Research* (formerly *Proceedings of the National Shellfisheries Association*) is the official publication of the National Shellfisheries Association

Journal of Shellfish Research
Volume 4, Number 2
ISSN: 00775711
December 1984

Journal of Shellfish Research, Vol. 4, No. 2, 113-117, 1984.

CHANGES IN THYMIDINE INCORPORATION BY LARVAE OF THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN) AFTER CHALLENGE BY TWO SPECIES OF YEAST (*CANDIDA*)

PHYLLIS C. BRAUN[1], THEODORE J. COMBS[1], AND WALTER J. BLOGOSLAWSKI[2]
[1]*Department of Biology*
Fairfield University
Fairfield, Connecticut 06430
[2]*National Marine Fisheries Service*
Northeast Fisheries Center
Milford Laboratory
Milford, Connecticut 06460

ABSTRACT Larval cultures of the American oyster *Crassostrea virginica* were challenged with the yeasts *Candida albicans* (Robin) and *C. tropicalis* (Castellani). After 48 hr, microscopic examination revealed abnormal shell development and reduced size for the oyster larvae. The results from autoradiographical studies using ^{3}H leucine indicate that *C. albicans* and *C. tropicalis* were ingested by the larvae. Oyster injury caused by the experimental yeasts was determined by measuring ^{3}H thymidine incorporation. During an 8-hr incubation, larvae challenged with various numbers of yeast cells exhibited a 16 to 78% decrease of ^{3}H thymidine incorporation compared to unchallenged control oysters. This test provides a simple and rapid measurement of metabolic injury.

KEY WORDS: *Candida, Crassostrea*, oyster, yeast, thymidine, shell development

INTRODUCTION

It has been reported that human-associated yeast cells are present in the waters of Long Island Sound (Combs et al. 1971). This finding was consistent with the report of Fell and Van Uden (1963) who noted that, in general, yeasts are found in littoral waters with high organic content. Furthermore, Buck et al. (1977) and Buck (1981) found a total of 28 species of human-associated yeasts in adult native populations of the American oyster *Crassostrea virginica* (Gmelin), the northern quahog *Mercenaria mercenaria* (Linné), and the blue mussel *Mytilus edulis* (Linné). The literature, however, reveals no studies that investigated a possible pathological association between yeast cells and bivalve molluscs. Such an association might be suspected as certain other fungal types are known to cause serious infections of commercially important bivalves, including *C. virginica* (Davis et al. 1954, Sindermann 1970).

In 1981, Combs et al. first reported significant alterations of oyster larvae due to challenge by *Candida* species. Radioactive-labeling techniques were also described in their report which became the impetus for the present investigation.

The purpose of this investigation was to determine whether two human-associated yeasts, *Candida albicans* (Robin) and *Candida tropicalis* (Castellani), were capable of interfering with the normal development of the larvae of *Crassostrea virginica* during an aquatic bioassay. The assay consists of exposing oyster larve to tritiated (^{3}H) thymidine in the presence of the appropriate yeast. By quantifying the rate of incorporation of an exogenously added, radioactive nucleoside, changes were observed in DNA synthesis. A similar technique was recently cited by Jackim and Nacci (1984) for embryos of the sea urchin *Arbacia punctulata* (Lamarck).

MATERIALS AND METHODS

Candida albicans and *Candida tropicalis*

Freshly transferred stock cultures of *Candida albicans* (ATCC 10231) and *Candida tropicalis* (ATCC 750) were grown at 37°C and maintained at 4°C on brain-heart infusion slants. In our laboratory, routine use of brain-heart infusion media extended the transfer time of these yeasts to 30 days versus 14 days for most other media. The inoculum for all experiments was obtained in the following manner: *C. albicans* or *C. tropicalis* were grown at 37°C for 18 hr on brain-heart infusion agar plates. Yeast cells were collected in 0.9% saline (wt/vol), centrifuged (3,000 x g, 4°C) for 10 min, washed twice, and then harvested and suspended in 0.9% saline. Yeast cells were counted using a hemocytometer.

Bioassays of *Crassostrea virginica*

The pathogenicity of each of the yeast isolates to freshly fertilized eggs of the American oyster was examined by bioassay of the resulting larvae. The initial step in the procedure was to inoculate yeasts on brain-heart infusion slants and incubate them overnight (18 to 24 hr) at 37°C. Broodstock oysters that were maintained at the NMFS

Milford Laboratory were induced to spawn by gradually raising the water temperature (Loosanoff and Davis 1963), and eggs were fertilized and counted. An inoculum of 15,000 freshly fertilized eggs was added to 1 l of Millipore-filtered, UV-treated seawater (MUVSW) in glass beakers kept in a constant-temperature incubator at 26°C as recommended by ASTM (1980). Subsequently, an appropriate inoculum of resuspended yeasts was added from the 0.9% saline solution to attain an initial concentration of 1.5 to 2.0 x 10^6 count-forming units per ml in the challenge beakers. Cultures were maintained for 48 hr, which allowed ample time for normal development to the straight-hinge, shelled veliger stage of *C. virginica*. Controls for the challenge beakers consisted of fertilized egg cultures without added yeast cells.

After 48 hr, cultures were sampled by screening the contents through a 36-μm nylon mesh screen, resuspending the trapped larvae in 200 ml of filtered seawater, then collecting a 2-ml aliquot, rinsing the pipet with 2 ml of seawater and preserving the sample with a few drops of 5% buffered formalin (Loosanoff and Davis 1963; Edwin Rhodes, NMFS Milford Laboratory, Milford, CT, pers. comm.). Samples were preserved as described above and examined with a compound microscope.

Larvae for challenge samples were counted and classified as normal or abnormal; normal larvae were "D"-shaped, which is typical for straight-hinge, 48-hr oyster larvae; abnormal larvae departed significantly from the normal "D" shape (Figure 1). Larvae were further classified as to whether they were alive or dead prior to fixing; live larvae have tissue with a darkened central gut and dead larvae are devoid of the tissue. The percent of normal development in experimental cultures was computed relative to that in control cultures and those isolates which caused greater than 80% mortality were considered suspect and examined further. Percent mortality was calculated as the number of surviving experimental larvae divided by number of live larvae in the control x 100.

Larvae were challenged with either yeast, *C. albicans* or *C. tropicalis*, in a larvae:yeast ratio of 1:100 for 48 hr of microscopically counted cells. Incorporation of ^{3}H leucine is a standard method of measuring protein synthesis (Bogoroch 1972). Using the larval oyster bioassay method described earlier, approximately 0.1 ml of each was viewed under light microscopy. Subsequently, 1 ml of each suspension (*C. albicans* or *C. tropicalis*, oyster larvae, *C. tropicalis* or *C. albicans* with oyster larvae) was placed on coverslips dipped in 1% bovine serum albumin and allowed to settle for 90 min (25°C). Tritiated (^{3}H) leucine (6 Ci/mmol - New England Nuclear, Boston, MA) was then added to each coverslip and incubated for an additional 30 min at 25°C. The incorporation of radioactive leucine was stopped with 95% ethanol. Each coverslip was dried and dipped into melted Ilford K-2 emulsion as described by Braun and Calderone (1978). Coverslips were exposed for 14 days (4°C) and then stained with 1% methylene blue.

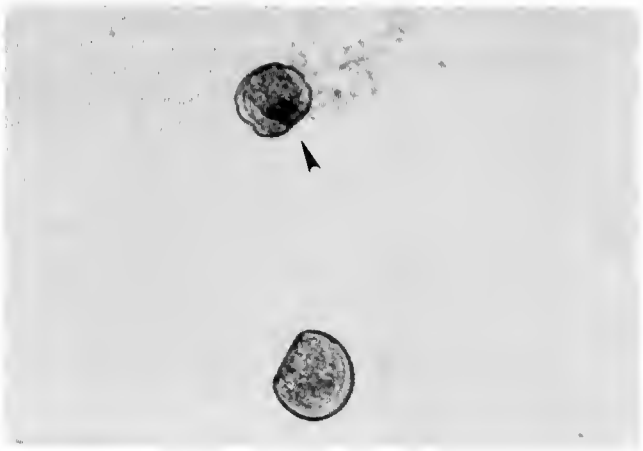


Figure 1. Photomicrograph of normal and abnormal (arrow) live larvae of *C. virginica* challenged with *C. albicans*. (x 100.)

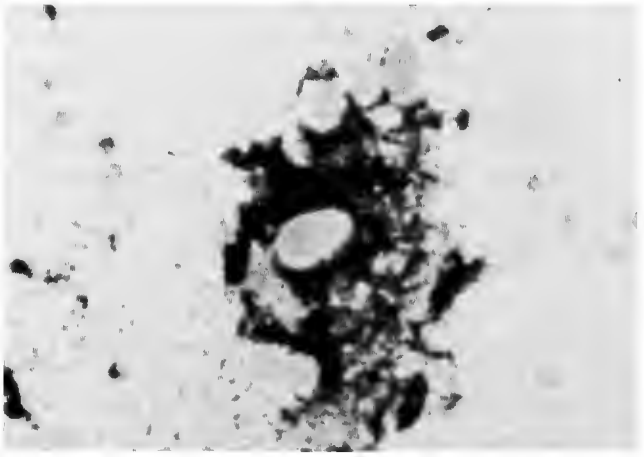


Figure 2a. Autoradiograph of TCA fixed, stained larvae with ingested *C. albicans* shown in pale blue. Leucine incorporation is shown as black spots in the larval tissue. (x 900.)

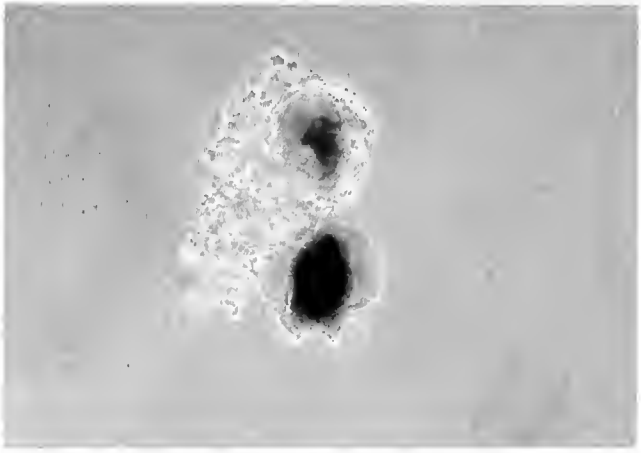


Figure 2b. Photomicrograph of two normal larvae of *C. virginica* treated with TCA. Note distorted shape and rupture of cellular content causing the spread of tissue shown in 2a. (x 400.)

Effect of *C. albicans* and *C. tropicalis* on Incorporation of ^{3}H Thymidine by *Crassostrea virginica*

Culture tubes contained a cell suspension of either *Crassostrea virginica* (1.2 x 10^3 cells), *Candida albicans*, *Candida tropicalis*, or both a yeast and larvae mixture in a total volume of 2 ml MUVSW. *Crassostrea virginica* was challenged with a yeast culture in 1:5, 1:100, and 1:1000 (larvae:yeast) ratio. All cultures were incubated with ^{3}H thymidine (101.0 Ci/mmol - New England Nuclear, Boston, MA) at 25°C. At designated intervals, duplicated cell suspensions were precipitated on ice with cold 15% trichloroacetic acid (TCA) and washed with absolute ethanol. Nonspecific trapping of label was determined by labeling cultures on ice and precipitating immediately with 15% TCA. Subsequently, all precipitated cultures were filtered onto glass fiber filters (Whatman GF/A) and washed with cold 95% ethanol.

All radioactive measurements were made using a Hewlett Packard Model 3380 liquid scintillation counter in scintillation liquid (0.1 g of p-bis [-5 phenyloxazolyl] benzene and 5 g of 2.5 diphenyloxazole dissolved in 1.0 *l* of scintillation grade toluene).

Calculations to determine the inhibitory effect of *Candida albicans* and *C. tropicalis* on incorporation of ^{3}H thymidine by *Crassostrea virginica* were as follows: the counts per minute (cpm) from the appropriate controlled yeast cultures were subtracted from the cpm obtained from the larval cultures and *C. albicans* or *C. tropicalis* incubated together. This figure representing *C. virginica* specific incorporation when incubated with a yeast was compared with the cpm obtained from cultures of *C. virginica* incubated without a yeast using the methods of Peterson and Calderone (1977).

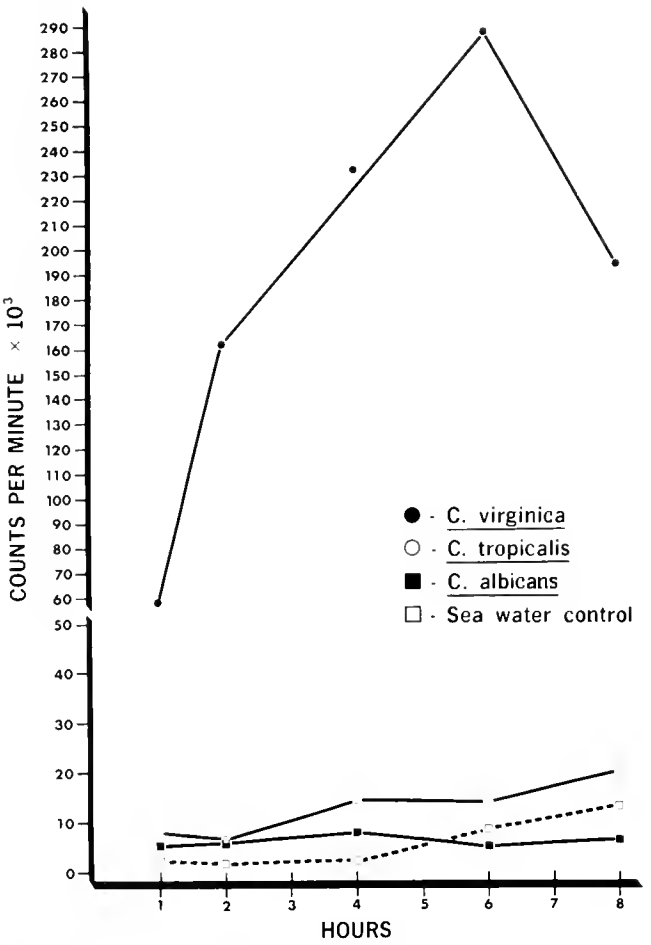


Figure 3. Incorporation of ^{3}H thymidine by larvae of *C. virginica*, *C. tropicalis*, *C. albicans* and seawater control.

RESULTS

After the 48-hr period, both challenged and unchallenged larvae were examined under light microscopy. Figure 1 represents the live normal unchallenged larva next to a larva that was challenged with *Candida albicans*. This live abnormal animal has impaired shell development and reduced size.

Autoradiographic studies of *Crassostrea virginica* showed that *Candida albicans* (Figure 2a) and *C. tropicalis* were ingested. Because of the TCA precipitation, the natural larval morphology was markedly altered (Figure 2b), and yeast cells were revealed in the gut area. It is evident from the heavy grain concentrations, which are indicative of leucine incorporation into tissue, that the challenged larvae continued to incorporate ^{3}H leucine after yeast ingestion. Comparisons between control larvae and challenged larvae for incorporation of this radioactive label indicated that protein synthesis by the challenged larvae did not appear to decrease. Both *Candida* species also incorporated ^{3}H leucine into their protein and after numerous slide examinations it was concluded that there was no decrease in grain development by the ingested yeasts when compared to controls.

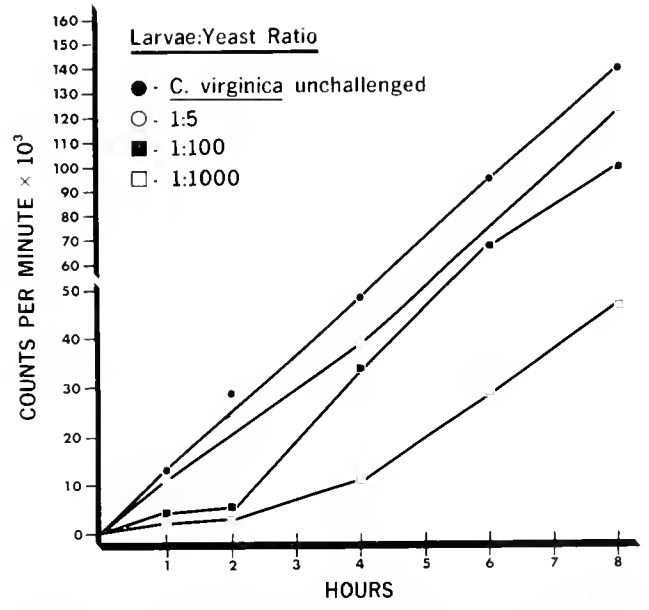


Figure 4. Incorporation of ^{3}H thymidine by *C. virginica* incubated with *C. albicans*.

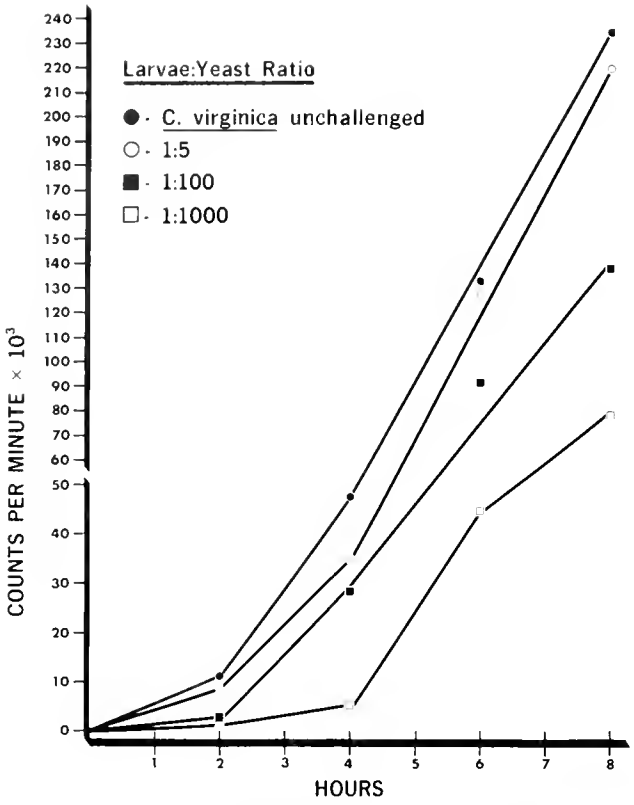


Figure 5. Incorporation of ^{3}H thymidine by *C. virginica* incubated with *C. tropicalis*.

These results suggest that ingestion of these yeasts by *C. virginica* caused no apparent injury to either *C. albicans* or *C. tropicalis*.

Tritiated Thymidine Incorporation

The results shown in Figures 3, 4, and 5 are the means of five separate trials. At individual time periods each trial was within ± 1000 cpm from the mean shown. Control studies were executed initially to determine the amount of ^{3}H thymidine incorporated by *Crassostrea virginica* and *Candida* species. An 8-hr study determined that the oyster larvae incorporated the majority of radioactive label, whereas approximately 5% of ^{3}H thymidine was incorporated into either of the yeasts (Figure 3). This small amount of radioactive label represents nonspecific binding of the ^{3}H thymidine to the surface of the yeasts. As shown in Figure 3, there was no significant incorporation of radioactive label by UV-filtered seawater alone.

The results shown in Figure 3 indicate that the *Candida* cells lacked a functional transport system for thymidine compared to the larvae. Therefore, change in thymidine incorporation by oyster larvae was considered to be an excellent method to measure yeast-induced injury. To quantify the effect of *Candida albicans* on *Crassostrea virginica*, various larvae:yeast ratios were used. As shown in Figure 4, significant decreases of nucleoside incorporation by *C. virginica* occurred. As the larvae:*C. albicans* ratio increases from 1:5, 1:100, and 1:1000, it reflects a mean decrease of ^{3}H thymidine incorporation of 16, 34, and 70%, respectively. After the 8-hr incubation, similar results were observed when *C. tropicalis* was employed as the challenge organism. Using the same larvae:yeast ratios, *C. tropicalis* inhibited the incorporation of radioactive thymidine by oyster larvae by means of 20, 40, and 78%, respectively (Figure 5).

DISCUSSION

The results presented herein indicate that the larvae-yeast association does produce abnormal development of larvae of *C. virginica*. We propose three possibilities that, at least partially, may account for the observed shell deformities. First, normal larval developmental mechanisms may have been altered by some byproduct of yeast metabolism. Second, since yeast cell walls, including *Candida* sp., contain highly polymerized glucans and mannans (Farkas 1979), it is possible that oyster larvae were unable to digest them (Tripp 1958, 1960) and, thus, abnormal shell development was simply one manifestation of a general pattern of starvation. Third, an invasion of larval tissue by yeast cells took place; in the case of *C. albicans* this explanation is unlikely because invasion is usually accompanied by germ tube development (Reynolds and Braude 1956). None was seen in this study.

The finding that incorporation of ^{3}H thymidine by larvae decreased with increases in yeast cell numbers strongly indicates that a larvae-yeast interaction did take place. Tritiated thymidine is an efficient and sensitive method to determine metabolic injury. This bioassay demonstrated a decrease in thymidine incorporation which is directly proportional to inhibition of DNA synthesis. It might also be emphasized that both *Candida* species produced similar decreases in the percentage of ^{3}H thymidine incorporated at comparable larvae:yeast ratios.

It is conceivable that metamorphosing larvae of *C. virginica* might be subject to the same type of injury as observed in this study since *C. albicans* and *C. tropicalis* gain entrance to marine waters through fecal pollution. This conclusion is underscored by the observation that as few as five yeast cells per larva—an attainable level found in contaminated waters—caused significant metabolic changes in the developing oyster.

ACKNOWLEDGMENTS

This work was partially supported by a Fairfield University Faculty Research Grant to P.C.B. and by U.S. Department of Commerce Contract No. NA-796-AC-00020 to T.J.C. The authors appreciate the technical help of Scott Wilson and the editorial assistance of Rita Riccio.

NOTE: Use of trade names in no way implies endorsement of commercial products by Fairfield University or the National Marine Fisheries Service.

REFERENCES CITED

American Society for Testing and Materials. 1980. Designation: E 724-80. Standard practice for conducting static acute toxicity tests with larvae of four species of bivalve molluscs. Philadelphia, PA: A.S.T.M.

Bogoroch, R. 1972. Liquid emulsion autoradiography. Gahan, P.B., ed. *Autoradiography for biologists.* New York: Academic Press. Chap. 5:123-150 p.

Braun, P. C. & R. A. Calderone. 1978. Chitin synthesis in *C. albicans*: comparison of yeast and hyphal forms. *J. Bacteriol.* 135:1472-1477.

Buck, J. D. 1981. Response of selected molluscan shellfish species to yeast exposure. Noank, CT: Univ. Connecticut, Marine Sciences Inst., Marine Research Lab. Final Report Contract No. NA-80-FA-C-00047:1-27.

———, P. M. Bubucis & T. J. Combs. 1977. Occurrence of human-associated yeasts in bivalve shellfish from Long Island Sound. *Appl. Environ. Microbiol.* 33:370-378.

Combs, T. J., P. C. Braun & W. J. Blogoslawski. 1981. Morphological alterations of larvae of the American oyster *Crassostrea virginica* when challenged with *Candida albicans* and *Candida tropicalis.* Abstracts of the 81st meeting of the American Society for Microbiology; Dallas, TX; March 1981; Vol. 10:174.

Combs, T. J., R. A. Murchelano & F. Jurgen. 1971. Yeasts isolated from Long Island Sound. *Mycologia* 63:178-181.

Davis, H. C., V. L. Loosanoff, W. H. Weston & C. Martin. 1954. A fungus disease in clam and oyster larvae. *Science* 120(3105): 36-38.

Farkas, V. 1979. Biosynthesis of cell walls of fungi. *Microbiol. Rev.* 43:117-144.

Fell, J. W. & N. Van Uden. 1963. Yeasts in marine environments. Oppenheimer, C. H., ed. *Symposium on marine microbiology.* Springfield, IL: Charles C. Thomas. p. 329-340.

Jackim, E. & D. Nacci. 1984. A rapid aquatic toxicity assay utilizing labeled thymidine incorporation in sea urchin embryos. *Environ. Toxicol. Chem.* 3:631-636.

Loosanoff, V. L. & H. C. Davis. 1963. Rearing of bivalve mollusks. *Adv. Mar. Biol.* 1:1-136.

Peterson, E. & R. A. Calderone. 1977. Growth inhibition of *Candida albicans* by rabbit alveolar macrophages. *Infect. Immun.* 15:910-915.

Reynolds, R. & A. Braude. 1956. The filament inducing property of blood for *Candida albicans:* its nature and significance. *Clin. Res. Proc.* 4:40-47.

Sindermann, C. J. 1970. Principal diseases of marine fish and shellfish, New York: Academic Press. p. 108-114.

Tripp, M. R. 1958. Studies on the defense mechanism of the oyster. *J. Parasitol.* 44(2):35-36.

Tripp, M. R. 1960. Mechanisms of removal of injected microorganisms from the American oyster, *Crassostrea virginica* (Gmelin). *Biol. Bull.* (Woods Hole) 119:210-223.

Journal of Shellfish Research, Vol. 4, No. 2, 119-124, 1984.

CULTURE OF THE NORTHERN HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ) IN A COMMERCIAL-SCALE, UPFLOW, NURSERY SYSTEM

JOHN J. MANZI[1], N. H. HADLEY[1], C. BATTEY[2], R. HAGGERTY[2], R. HAMILTON[2], AND M. CARTER[2]

[1]*Marine Resources Research Institute*
P. O. Box 12559
Charleston, South Carolina 29412 (U.S.A.)
[2]*Trident Seafarms Co.*
Folly Beach, South Carolina 29439
Contribution No. 198 from the South Carolina Marine Resources Center.

ABSTRACT Upflow nursery systems for culture of bivalve mollusc seed are attractive alternatives to traditional raceway systems. The potential benefits include maximizing space utilization, low construction cost, ease of maintenance, and operational longevity. A commercial nursery facility for raising *Mercenaria mercenaria* in South Carolina employs both forced and passive upflow culture instead of traditional raceway systems. This paper reports results from the first year of operation of this upflow nursery system. Seed clam growth is analyzed in relation to clam density, water flow, and environmental parameters, and performance of passive- and forced-flow systems is compared. Biomass increases as high as 1400% per month were achieved in forced flow systems at stocking densities of 0.3 to 0.5 $g \cdot cm^{-2}$ and flow rates of 80 to 120 $l \cdot min^{-1} \cdot kg^{-1}$. In passive flow systems, biomass increases as high as 800% per month were achieved at stocking densities of 0.2 to 0.6 $g \cdot cm^{-2}$ and flow rates of 23 to 117 $l \cdot min^{-1} \cdot kg^{-1}$. Results were compared with those from raceways and from an experimental-scale, passive upflow system.

KEY WORDS *Mercenaria*, hard clam, nursery culture, mariculture

INTRODUCTION

A cooperative project, involving both private and public resources, was initiated in August 1980 to develop commercial mariculture of the northern hard clam *Mercenaria mercenaria* (Linné) in South Carolina. A commercial-scale mariculture facility was established on Folly Island, near Charleston, SC (Figure 1). The facility uses a two-step culture program to produce hard clams. Small seed clams ($\sim$ 1 mm) are imported from commercial hatcheries and reared to field planting size (7 to 8 mm) in a land-based nursery. Seed clams are then transferred to intertidal field units (cages and pens) for growout to market size (44 to 50 mm).

The land-based nursery initially used traditional raceway culture techniques but converted to upflow culture exclusively in 1982. Upflow bivalve culture has been widely applied in Europe (Bayes 1981, Lucas and Gerard 1981) but has only recently received attention in the United States (Manzi and Whetstone 1981, Manzi et al., In Press). Upflow systems utilize a vertical water flow that is directed up through a bivalve seed mass, rather than horizontally across the seed clams as in raceway culture. Two different upflow systems, referred to here as forced (or active) and passive, have been developed and are in common use (Figure 2). Forced systems generally consist of closed-bottom cylinders plumbed to receive water, under pressure, directly below an intermediately positioned screen of appropriate mesh to retain a seed mass. The water is forced up through the screen, partially fluidizing the seed mass, and eventually overflows through drains at the top of the cylinder. Passive

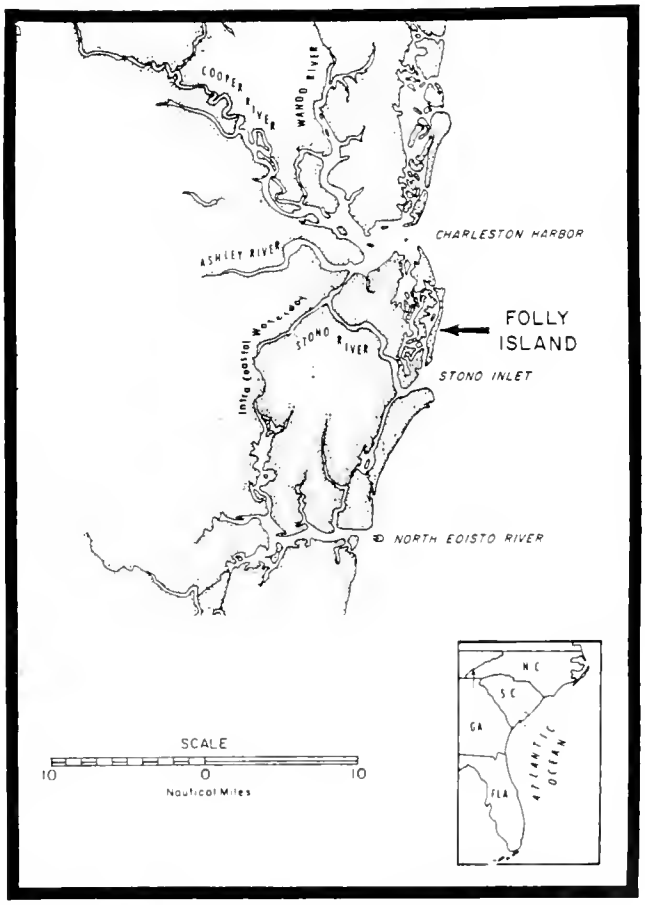


Figure 1. Map showing location of Trident Seafarms Company nursery on Folly Island, SC.

systems employ open-ended containers (cylinders or boxes) suspended in a reservoir of sufficient size and configuration. A screen of appropriate mesh size forms the bottom of each container and supports the seed mass, often several centimeters thick. Water is introduced into the reservoir and overflows only through drains located in the upper section of each container (Figure 2). Reservoir water is thus drawn up through the containers, accelerating rapidly as it passes through the seed mass and decelerating upon reaching the overlying pool between the surface of the seed mass and the drain. If flow rates are sufficient, wastes and silt are swept through the seed mass and settle as a loose layer at the seed mass surface.

Upflow culture systems appear to create conditions that are conducive to rapid growth (Rodhouse and O'Kelly 1981) while providing distinct advantages over raceways, including ease of maintenance, effective utilization of space, longevity of service, and economy of construction (Bayes 1981, Manzi et al. In Press). This paper describes an upflow nursery system and reports growth data from the first season of operation.

MATERIALS AND METHODS

The land-based nursery, located on Folly Island, SC (Figure 1), consisted of 60 forced-flow cylinders, arranged in banks of 20, and 160 passive-flow cylinders, contained in 20 reservoir tanks. A 25-hp centrifugal pump was used to pump water at a rate of 360 $m^3 \cdot h^{-1}$ (1600 $gal \cdot min^{-1}$) from below the surface of the Folly River approximately 100 m to the nursery pad through 20-cm (ID) PVC pipe. Feeder pipes (5-cm ID) fitted with ball valves were located at intervals along the nursery pad to provide adjustable water flow to reservoir tanks and forced-flow cylinders. Effluent water was directed to concrete sluices running the length of the pad and spilling into a catch basin (∿ 1.5 m x 17 m) which drained into a small creek.

Forced, or active upflow cylinders were constructed of 20-cm (ID) PVC pipe fitted with a slip cap on one end and a nylon screen (710 or 1000-μm mesh) at an intermediate position. Water was introduced through a 2.5-cm elbow on the side of the bottom cap and exited via a 5-cm drain located near the top of the unit. Water was fed to a bank of 10 such units through a PVC manifold equipped with 2.5-cm gate valves, allowing individual control of the flow to each cylinder. Flow rates to each cylinder were 11 to 15 $l \cdot min^{-1}$. These forced upflow cylinders were used for very small seed clams (∿3 mm SL). As water was forced up through the screen, the entire seed mass was partially fluidized. A layer of seed clams initially < 1 cm thick became 5 to 6 cm thick when fluidized. That fluidization assured water flow to all areas of the seed mass and resulted in rapid, uniform growth. Seed clams (1 to 2 mm SL) were stocked at a density of 100 to 300 g $cylinder^{-1}$ (0.3 to 1.0 $g \cdot cm^{-2}$). For 1-mm clams, the biomass represented 100,000 to 300,000 $clams \cdot cylinder^{-1}$ (300 to 1000 $clams \cdot cm^{-2}$). As the seed clams grew they were redistributed

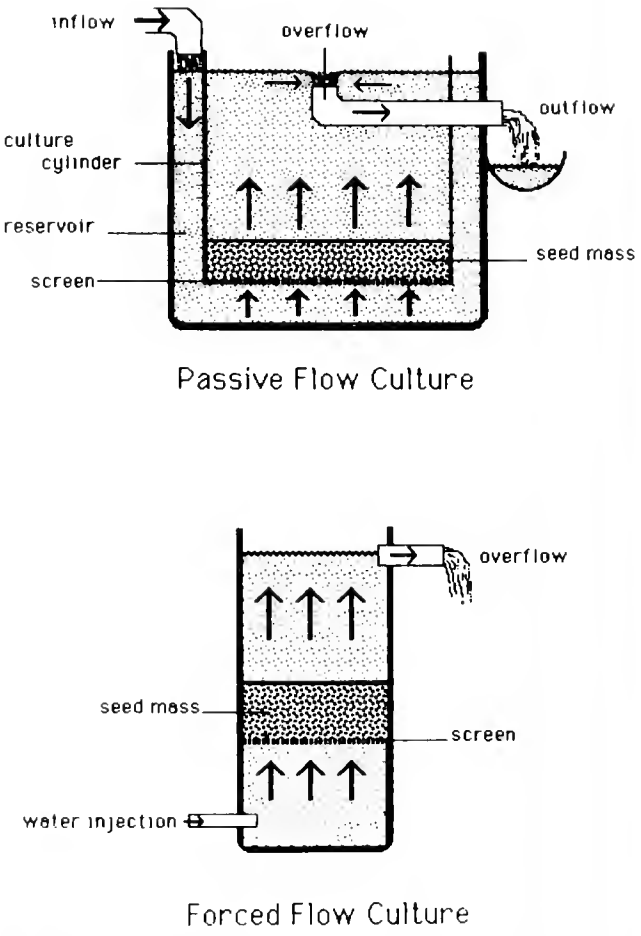


Figure 2. Diagrammatic representation of forced and passive upflow cylinders.

to maintain a biomass of 200 to 400 $g \cdot cylinder^{-1}$ (0.6 to 1.2 $g \cdot cm^{-2}$).

As the clam size increased the fluidizing became less effective and the seed clams were transferred to larger diameter, passive upflow cylinders. These were constructed of PVC duct pipe (46- or 56-cm d) with a nylon screen (710- or 1600-μm mesh) stretched across the bottom. Eight such cylinders were suspended in a reservoir (∿6 m x 0.6 m) which received a flow of approximately 240 to 300 $l \cdot min^{-1}$. Water left the reservoir via 5.0-cm drains located in the upper portion of each cylinder that passed through the sidewall of the tank to a common trough. Flow to each cylinder was approximately 30 to 35 $l \cdot min^{-1}$. Passive cylinders (56-cm d) were initially stocked at a density of 500 to 850 $g \cdot cylinder^{-1}$ (0.2 to 0.35 $g \cdot cm^{-2}$). For 3-mm seed clams that biomass was equivalent to 50,000 to 85,000 $seed \cdot cylinder^{-1}$ (20 to 35 $seed \cdot cm^{-2}$). Seed clams were redistributed at regular intervals to maintain a biomass of 0.85 to 1.5 $kg \cdot cylinder^{-1}$. Final biomass in those cylinders when clams reached 7 mm ranged from 2 to 5 kg (0.8 to 2.0 $g \cdot cm^{-2}$).

All passive and forced-flow units were drained and rinsed daily. Seed clams were culled and redistributed once every 2 to 4 wk. Culling was accomplished by sieving the seed on

appropriate standard screens ranging from 1.18- to 4.75-mm mesh. Seed clams were transferred to passive cylinders when large enough to be retained on a 2.0-mm screen and moved to field planting units when retained on a 4.75-mm screen. Intermediate screen sizes were used to remove shell and debris and to segregate seed clams into different size fractions. Each time that the seed clams were culled, measurements of length and settled volume were made and increases in length and biomass were determined. Time intervals between culling varied; therefore, biomass increases were converted to an equivalent monthly per cent increase (% MBI) using the formula:

$$\% \text{ MBI} = \frac{B_f - B_i}{B_i} \times 100 \times \frac{30}{T}$$

where B_f is the final biomass in grams, B_i is the initial biomass in grams, and T is the period of culture in days.

RESULTS AND DISCUSSION

The upflow nursery had a theoretical capacity at any one time of 4 to 16 x 10^6 seed clams, depending on seed size. An idealized stocking scheme and expected production for one season (April-November) are presented in Table 1a. Assuming that 16 x 10^6 seed clams (∿ 1 mm initial length, ∿ 1000 clams·g^{-1}) were imported over a 12- to 16-wk period commencing in April and 75% survived to a planting size of 7.0 mm (∿8 clams·g^{-1}), net production would be 1480 kg (9250% increase in biomass) for a 9-mo period. The nursery would be operating at maximum capacity from mid-May through August. Additional seed clams could be purchased in the fall and held through the winter to plant in early spring, which would represent an ideal situation.

The nursery became operational in the fall of 1982. In 1983 seed clams were imported in April, May, and July from commercial hatcheries in New England. A total of 16.34 x 10^6 seed (11.98 kg) were imported at an average size of 1.5 mm. Seed clams remained in the nursery until they were approximately 7 mm in length. From April to December 1983, 3.47 x 10^6 seed clams (768 kg) were transferred from the nursery to field culture units. At the end of December, 3.4 x 10^6 clams (215 kg) remained in the nursery. Net production for the year was 813 kg with approximately 38% survival (Table 1b).

Low production and poor survival were largely attributed to the poor stocking schedule. Hatcheries were unable to comply with the desired importation schedule. As a result, only 3.82 x 10^6 seed clams were received during the ideal stocking time (April-June) while 12.66 x 10^6 seed clams were received in a 2-wk period in July, when water temperatures

TABLE 1.

Comparison of ideal (A) and actual (B) stocking and production schedules for a commercial upflow nursery system in South Carolina.

A. IDEALIZED STOCKING SCHEDULE.

Month	Input		Output		Residual		Net Production	Space Utilization
	# Seed (million)	Biomass (kg)	#Seed (million)	Biomass (kg)	# Seed (million)	Biomass (kg)	(kg)	% of total
April	4	4			3.8	7.6	3.6	4
May	4	4			7.4	25.6	14.0	25
June	4	4	0.5	62.5	10.3	54.6	87.5	59
July	4	4	1.2	150.0	12.3	104.6	196.0	94
August			2.2	275.0	9.4	142.0	312.4	100
September			2.8	350.0	6.0	144.0	352.0	98
October			2.5	312.5	3.1	115.0	283.5	66
November			1.8	225.0	1.1	65.0	175.0	31
December			0.8	100.0	0.2	20.0	55.0	8
Total	16	16	11.8	1475.0	0.2	20.0	1479.0	

B. ACTUAL 1983 STOCKING SCHEDULE.

March	1.32	158.65*			1.32	158.65*		68
April	1.26	1.54	0.395	89.3	1.41	59.58	-11.31	20
May	2.42	2.15			3.06	51.46	-10.27	33
June			0.200	24.6	1.58	37.49	10.63	27
July	12.66	8.29	0.735	163.5	15.22	89.30	207.02	75
August			0.230	125.0	12.96	227.00	262.70	100
September			0.746	189.3	9.89	247.00	209.30	100
October			0.564	93.1	5.60	267.00	113.30	100
November					3.91	255.50	-11.66	97
December			0.596	83.2	3.40	215.40	43.05	92
Total	17.66	170.63	3.466	768.0	3.40	215.40	812.75	

*Carried over from previous stocking

TABLE 2.

Mean monthly growth (%MBI) after 30 and 60 days of culture for seed clams stocked at different times of year in three types of upwelling units in a commercial clam nursery in South Carolina.

		STOCKING DATE									
		4/8		5/12		5/25		7/2		7/12	
Unit Type	Days	Growth (%MBI)	Temp. (°C)	Growth (%MBI)	Temp. (°C)	Growth (%MBI)	Temp. (°C)	Growth (%MBI)	Temp. (°C)	Growth (%MBI)	Temp. (°C)
20-cm forced flow	30	309	19	341	23	538	25	950	29	1147	30
	60	277	21	295	24	—	—	693	30	466	29
46-cm passive flow	30	—	—	—	—	575	27	717	29.5	416	29
	60	—	—	—	—	—	—	393	29.5	323	29
56-cm passive flow											
Seed < 3 mm	30	—	—	—	–	503	25	282	30	449	29
	60	—	—	—	—	—	—	—	—	311	29
Seed > 3 mm	30	203	24	276	26	336	28	192	29.5	200	29
	60	187	25	268	28	243	28	115	27	155	26

TABLE 3.

Comparison of seed growth in raceways and passive-upflow units in relation to stocking density and water flow rate. (% MBI indicates mean percentage increase in biomass per month.)

Raceways[1]			Upwelling Units					
			10-cm diameter[2]			56-cm diameter		
Density ($g \cdot cm^{-2}$)	Flow ($l \cdot min^{-1} \cdot kg^{-1}$)	Growth (%MBI)	Density ($g \cdot cm^{-2}$)	Flow ($l \cdot min^{-1} \cdot kg^{-1}$)	Growth (%MBI)	Density ($g \cdot cm^{-2}$)	Flow ($l \cdot min^{-1} \cdot kg^{-1}$)	Growth (%MBI)
0.0017	1483	132	0.25	118	122	0.21	76	170
0.0051	507	105	0.50	58	126	0.42	38	137
0.0153	169	126	1.00	30	126	0.63	25	132
0.0459	56	125	1.00	26	120			
			2.00	15	99			
			2.00	14	113			
			3.00	9	78			
			4.00	7	73			

[1]Data from Hadley and Manzi (1984)
[2]Data from Manzi et al. (In Press)

were very high (29-30°C). The forced-flow cylinders were not able to accommodate all of the small seed clams that were received in July, and some had to be stocked directly in passive upflow cylinders. No additional space was available for redistribution and the clams remained in both passive and forced-flow cylinders for up to 48 days without being thinned. The nursery was stocked below capacity during the spring growth period and at or near 100% capacity from August through November (Table 1b).

A number of factors influenced growth rate of seed clams in the nursery system. These included water temperature, flow rate and stocking density. The effect of temperature on growth is apparent from Table 2. As previously reported (Manzi et al. In Press, Hadley and Manzi 1984) growth of seed clams > 3 mm was reduced at temperatures exceeding 28-29°C. This did not appear to be the case with very small seed clams (< 3 mm) that were stocked in active flow cylinders (Table 2). Apparently the high flow rates and fluidizing effect attained in these cylinders fostered growth even under these extreme temperature conditions.

Previous data from raceways (Hadley and Manzi 1984) and experimental-scale upwelling cylinders (Manzi et al. In Press) indicated that growth rate was directly related to water flow per unit biomass of seed clams. Growth rates of 4-mm clams at various densities were determined in April 1983 in 56-cm cylinders in the commercial nursery. These observations were compared with data taken in April 1981 in experimental raceways and April 1982 and 1983 in 10-cm cylinders (Table 3). Mean monthly rates of biomass increase (MBI) in commercial-scale cylinders (56-cm d) ranged from 132 to 170% (MBI) at flow rates of 25 to 76 $l \cdot min^{-1} \cdot kg^{-1}$ and water temperature of 18°C. Mean growth rates in 10-cm experimental cylinders varied from 73 to 126% (MBI) at temperatures of 16 to 18°C and flow rates ranging from 7 to 118 $l \cdot min^{-1} \cdot kg^{-1}$ (Manzi et al. In Press). In experimental raceways, seed grew at mean rates of 125 to 132% (MBI) at water temperatures of 13 to 16°C and flow rates of 56 to 1483 $l \cdot min^{-1} \cdot kg^{-1}$ (Hadley and Manzi 1984). During the 1983

production season, mean growth rates in passive flow cylinders in the commercial nursery ranged from 115 to 336% (MBI) at temperatures of 24 to 29.5°C and flow rates ranging from 17 to 117 $l \cdot min^{-1} \cdot kg^{-1}$ (Table 2). The highest mean monthly growth rates in the commercial nursery (Table 2) exceeded those in experimental upflows (Manzi et al. In Press) and raceways (Hadley and Manzi 1984), but the mean raceway performance over a range of stocking densities was somewhat higher than upflow performance. This may be an artifact of the experimental design of the raceway system, which used very low densities (0.002 to 0.05 $g \cdot cm^{-2}$) and high flow rates (52 to 1483 $l \cdot min^{-1} \cdot kg^{-1}$).

Growth rates in the different types of upflow cylinders were used to determine appropriate stocking densities (Table 4). These densities were appropriate for this particular system, but carrying capacities of any nursery necessarily depend on site-specific factors such as available food, ambient temperatures, and pumping capacity. Results from this system may serve as general guidelines or points of departure for other areas. In this nursery, forced-flow cylinders could be stocked at 0.31 to 0.46 $g \cdot cm^{-2}$, depending on seed clam size (Table 4). Resultant flow rates were approximately 80 to 120 $l \cdot min^{-1} \cdot kg^{-1}$. Seed clams had to be redistributed frequently (every 2 wk), so that the density did not exceed 1.1 to 1.2 $g \cdot cm^{-2}$ and a minimum flow rate of 30 $l \cdot min^{-1} \cdot kg^{-1}$ was maintained. Seed clams of < 2 mm did not grow well in passive upflow cylinders. Small seed clams of this size extruded byssal threads and tended to clump together. That clumping resulted in uneven distribution in the large-diameter, passive cylinders, and "fountaining" occurred, with the water taking the path of least resistance while other areas of the cylinder received little flow. Slightly larger seed clams (2 to 3 mm) grew rapidly in passive upflow cylinders if stocking densities were low (and thus flow rates high). Appropriate initial stocking densities were 0.18 $g \cdot cm^{-2}$ for 46-cm cylinders and 0.16 $g \cdot cm^{-2}$ for 56-cm cylinders; these resulted in flow rates that were similar to those provided by forced-flow cylinders (~80 to 120 $l \cdot min^{-1} \cdot kg^{-1}$) (Table 4). Seed clams were redistributed frequently, sometimes as often as once a week, to maintain a density of not more than 0.6 to 0.7 $g \cdot cm^{-2}$ and a flow rate of at least 23 to 30 $l \cdot min^{-1} \cdot kg^{-1}$. Larger seed clams were stocked at higher densities than the very small clams because of space constraints. Growth rates were not as rapid, but that may have been partly a function of the natural decrease in rate of growth with increasing size. Initial stocking densities and redistribution densities used for seed clams 3 to 6 mm in length are listed in Table 4. In general, seed clams could be left in the cylinder until the volume doubled and then redistributed to reduce the biomass to an appropriate density.

In summary, results from the first season of operation of a commercial-scale, upwelling nursery indicated that seed clams grew rapidly in this type of system. Forced-flow cylinders stocked at 0.31 to 0.46 $g \cdot cm^{-2}$ and supplied with water at flow rates of 80 to 120 $l \cdot min^{-1} \cdot kg^{-1}$ were most effective for growth of seed clams of < 3 mm in length. Passive upflow cylinders could be used for 2- to 3-mm seed clams if densities were kept low, resulting in flow rates per unit biomass similar to those provided by forced upflow cylinders. Seed clams of > 3 mm length were stocked in passive upflow cylinders at densities of 0.2 to 0.6 $g \cdot cm^{-2}$ (depending on seed size) and with water flow rates of 23 to 70 $l \cdot min^{-1} \cdot kg^{-1}$. Seed clams grew from 1 to 7 mm in 60 to 120 days. Biomass increases were as high as 1400% (MBI) in forced-flow cylinders and 800% (MBI) in passive-flow cylinders, and compared favorably with growth rates reported previously for passive-upflow cylinders and raceways.

Poor survival in this first season can be attributed, at least in part, to factors which could be eliminated with better planning. The most important factors in determing overall production of a nursery appear to be a carefully planned importation schedule of seed clams and attention to proper stocking densities. This would avoid overcrowding, especially during periods of high water temperature, and take

TABLE 4.
Appropriate stocking densities and flow rates for different sizes of seed clams in different types of upflow units in a commercial nursery system in South Carolina.

Unit Type	Diam.	Flow rate	Velocity	Seed size	Initial density		Initial flow	Final Density		Final flow
	(cm)	($l \cdot min^{-1}$)	($cm \cdot sec^{-1}$)	(mm)	(ml seed/ unit)	($g \cdot cm^{-2}$)	($l \cdot min^{-1} \cdot kg^{-1}$)	(ml seed/ unit)	($g \cdot cm^{-2}$)	($l \cdot min^{-1} \cdot kg^{-1}$)
Forced flow	20	12	0.62	< 2	100	0.31	120	350	1.08	34
				2-3	150	0.46	80	400	1.23	30
Passive flow	46	35	0.36	< 2	NR*	—	—	—	—	—
				2-3	300	0.18	117	1200	0.73	29
Passive flow	56	35	0.24	< 2	NR*	—	—	—	—	—
				2-3	400	0.16	80	1500	0.62	23
				3	500	0.20	70	1600	0.65	22
				4	850	0.35	41	1700	0.69	21
				5	1150	0.47	30	2000	0.82	18
				6	1500	0.61	23	3000	1.24	12

*NR = Not recommended for this size seed.

advantage of the spring and fall growth periods. In order to assure that the stocking schedule is maintained, it would be most desirable to control seed production, thus eliminating dependence on commercial hatcheries in other states where environmental conditions differ and may delay seed importation.

ACKNOWLEDGMENTS

The authors are grateful to Trident Seafarms Company for allowing site use and making production data available for this study. We should like to thank Drs. P. J. Eldridge and V. G. Burrell, Jr. and Mr. Bill Anderson for reviewing the manuscript, Ms. Karen Swanson for help with figure preparation, and Ms. Nancy Beaumont for assistance with preparation of the tables and typescript. This research was supported by NOAA-Office of Sea Grant through the South Carolina Sea Grant Consortium.

REFERENCES CITED

Bayes, J. C. 1981. Forced upwelling nurseries for oysters and clams using impounded water systems. Claus, C., DePauw, N., and E. Jaspers, eds. *Nursery Culturing of Bivalve Molluscs.* Bredene, Belgium: European Mariculture Society Special Publication 7:73-82.

Hadley, N. H. & J. J. Manzi. 1984. Growth of seed clams (*Mercenaria mercenaria*) at various densities in a commercial scale nursery system. *Aquaculture* 36:369-378.

Lucas, A. & A. Gerard. 1981. Space requirement and energy cost in some types of bivalve nurseries. Claus. C., DePauw, N., and Jaspers, E., eds. *Nursery Culturing of Bivalve Molluscs.* Bredene, Belgium: European Mariculture Society Special Publication 7:151-170.

Manzi, J. J. & J. M. Whetstone. 1981. Intensive hard clam mariculture: a primer for South Carolina watermen. Charleston, SC: South Carolina Sea Grant Consortium. Mar. Adv. Publ. 81-01:20 p.

Manzi, J. J., N. H. Hadley & M. B. Maddox. In Press. Seed clam *Mercenaria mercenaria* culture in an experimental-scale upflow nursery system. Submitted to *Aquaculture.*

Rodhouse, P. G. & M. O'Kelly. 1981. Flow requirements of the oysters *Ostrea edulis* and *Crassostrea gigas* Thunb. in an upwelling column system of culture. *Aquaculture* 22:1-10.

Journal of Shellfish Research, Vol. 4, No. 2, 125-129, 1984.

GROWTH AND SURVIVAL OF THE NORTHERN HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ) FROM GEORGIA, VIRGINIA, AND MASSACHUSETTS IN COASTAL WATERS OF GEORGIA

RANDAL L. WALKER[1] AND CELESTE M. HUMPHREY[2]
[1]*Skidaway Institute of Oceanography*
P. O. Box 13687
Savannah, Georgia 31416
[2]*Department of Biology*
Dalton Junior College
Dalton, Georgia 30720

ABSTRACT Growth and survival of three stocks of northern clam *Mercenaria mercenaria* from Georgia, Virginia, and Massachusetts planted in coastal waters of Georgia were compared. Clams were planted in predator-exclusion cages at 1000 clams m^{-2} at a mean initial shell length of 10.4, 11.0, and 12.8 mm for the Georgia, Virginia, and Massachusetts stocks, respectively. Georgia clams grew from 10.4 to 28.7 mm in the first year and 45.2 mm in the second year. Virginia clams grew from 11.0 to 36.9 mm in the first year to 51.6 mm after 2 years. The Virginia and Georgia stocks reached commercial size (44.4 mm) in 24 and 33 mo, respectively. Massachusetts clams grew from 12.8 to 23 .9 mm in the first year. First year survival for Georgia, Virginia, and Massachusetts stocks was 29%, 31%, and 14%, respectively. No significant difference in survival between stocks was observed because of high within-treatment variation (Analysis of Variance $\alpha = 0.05$). Survival in the second year for Georgia, Virginia, and Massachusetts stocks was 64%, 8%, and 0%, respectively. Mortalities in the first year resulted from blue crab and common mud crab predation; whereas, second year mortalities resulted from storm activities.

KEY WORDS: *Mercenaria mercenaria*, hard clams, growth, survival

INTRODUCTION

The coastal waters of Georgia contain approximately 182,100 ha (450,000 a) of salt marsh, approximately 33% of the salt marshes of the Atlantic seaboard. In the early part of this century, these marshes supported large oyster and small clam fisheries. Today, the oyster industry is almost non-existent (Harris 1980) and clam harvesting is sporadic (Walker et al. 1980, Walker and Tenore 1984, Walker 1984a). This is unfortunate because most of the coastal waters of Georgia are relatively free of pollution and are suitable for commercial culture of shellfish.

As more northern waters are closed to shellfishing because of pollution (National Marine Fisheries Services 1977) the opportunity for utilizing the coastal waters of Georgia for culturing shellfish becomes more attractive. Northern clams grow rapidly and throughout the year in southern waters (Menzel 1963). In South Carolina and Georgia growth varies seasonally (Eldridge et al. 1976, Walker 1984b), whereas in Florida, clam growth is most rapid in fall and spring, less in winter, and slowest in summer (Menzel 1963, 1964). At the northern limit of its range, growth in *M. mercenaria* ceases during the winter when water temperatures reach 5 to 6°C (Loosanoff 1939), and the major growth occurs primarily in the summer when water temperatures reach 20°C (Ansell 1968).

Numerous studies have compared growth rates of *M. mercenaria*, the southern hard clam *Mercenaria campechiensis* (Gmelin), and their hybrids, but growth studies using different hatchery stocks of the same species are few. When grown under similar conditions in different locales, *M. campechiensis* outgrows *M. mercenaria* and their hybrids regardless of locale (Chesnut et al. 1957, Haven and Andrews 1957, Menzel 1963, 1964, Woodburn 1963, Roels et al. 1976). Although *M. campechiensis* and hybrids grow faster than *M. mercenaria* in northern waters, heavy mortality losses occur (Chesnut et al. 1957, Haven and Andrews 1957). Such variations in growth and survival of clam stocks are worthy of consideration in developing a hatchery-based clam fishery. One option for the development of a hard clam fishery in Georgia is through purchase and planting of seed clams from out-of-state hatcheries. In order to evaluate this option it was necessary to compare the growth and survival rates of different regional hatchery stocks of *M. mercenaria*, grown under similar conditions, in Georgia waters. This paper describes the results of those growth trials.

MATERIALS AND METHODS

The growth of three stocks of hard clams from Georgia, Virginia, and Massachusetts stocks were compared. Georgia clams were collected from Cabbage Island near Savannah, GA, and shipped to the Virginia Institute of Marine Science, Eastern Shore Laboratory, Wachapreague, VA, where they were spawned and cultured to a mean shell length (anterior-posterior dimension) of 10.4 + 1.2 (S.D.) mm before their

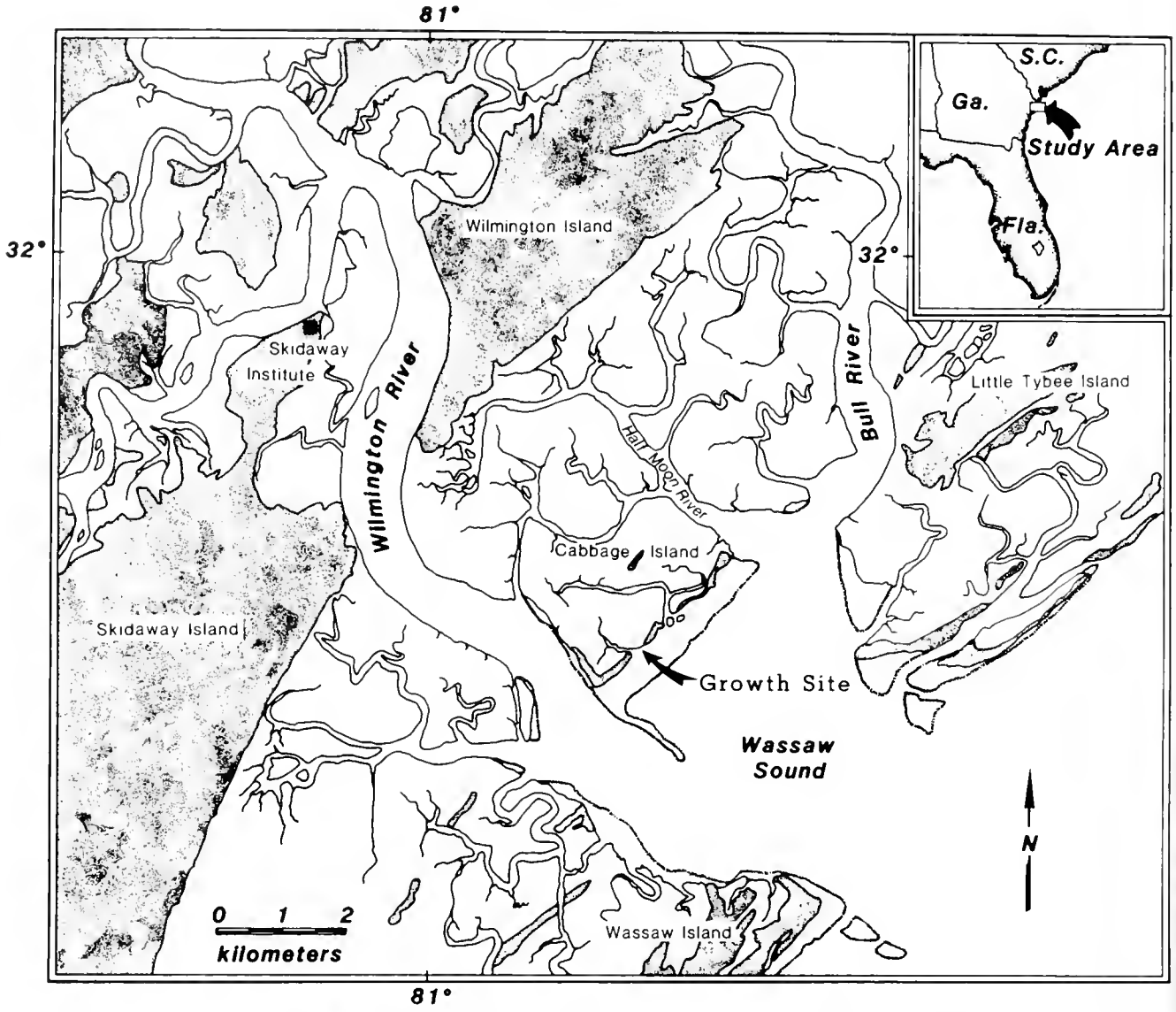


Figure 1. Map of Wassaw Sound, Georgia, showing experimental growth site.

return to Georgia. The Wachapreague laboratory also supplied a fast growing stock of Virginia clams with a mean shell length of 11.0 + 1.2 (S.D.) mm. A third stock (12.8 + 1.8 [S.D.] mm length), also selectively bred for rapid growth, was obtained from Martha's Vineyard Shellfish Group, Oak Bluffs, MA. Clams were planted on 30 September 1980 near Cabbage Island (Figure 1) in 1- x 1- x 0.3-M (LxWxH) cages constructed of 6-mm mesh vexar plastic. The cages were buried in a sandy substrate to a depth of 0.15 m and the enclosed bottom surface was layered with 5 cm of gravel aggregate in an attempt to control crab predation (Castagna and Kraeuter 1977). A 1-m long stake was attached to each corner of each cage to help hold the cages in place.

The percentage of sand, silt, and clay in substrates enclosed in each cage were determined by gravimetric measures (Folk 1974) in September 1980. Clams were planted in substrates of 80% sand, 15% silt, and 5% clay, with a 5-cm layer of gravel atop the substrate. Shifting sands buried the gravel within a month after it was laid down. Clams then migrated into the newly formed sand layer atop the gravel where crabs could prey on them.

Three replicates of each stock were planted at a density of 1000 clams·m^{-2}. After seeding, the cages were covered with tops constructed of 6-mm mesh vexar plastic to prevent the entry of blue crabs (*Callinectes sapidus* Rathbun) and common mud crabs (*Panopeus herbstii* H. Milne Edwards).

Cages were sampled seasonally for 2 years. All sediment contained within the cage to a depth of 0.15 m was sieved through 4-mm screen. Clams were counted and measured for shell length to the nearest 0.1 mm with vernier calipers. Sediment and clams were then returned to their respective plots.

To minimize the effect of clam density upon growth (Eldridge et al. 1979, Walker 1984b), clams of each stock

were removed from cages, counted, measured, and redistributed at approximately equivalent densities in September 1981. The Georgia stock was redistributed into six cages at 125 clams per cage; the Virginia stock into eight cages at 100 clams per cage; and the Massachusetts stock into three cages at 100 clams per cage. Furthermore, 126, 139, and 115 clams from the Georgia, Virginia, and Massachusetts stocks, respectively, were sacrificed for genetic studies (Humphrey, unpublished data).

RESULTS

First year survival of seed clams from Georgia, Virginia, and Massachusetts stocks was 29, 31, and 14%, respectively (Table 1). These differences were not significant because of high within-treatment variation (Analysis of Variance [ANOVA] $\alpha = 0.05$). Heaviest mortality of all stocks occurred between April and July (Table 1).

The Georgia, Virginia, and Massachusetts stocks had a 64, 8, and 0% survival, respectively, in the second year (Table 1). Mortality in the second year resulted primarily from storm activity. All of the Massachusetts clams were lost in late September and cages containing the other two stocks were damaged during the same period. Surviving clams were transplanted to new cages. Of the Georgia clams, 125 were killed by burial of one cage by shifting sands during the September storm. Another cage containing 125 Georgia clams was washed away between December 1981 and March 1982. Of the 269 Georgia clams killed between September 1981 and September 1982, 93% died from storm-related factors and 7% died from crab predation (as evidenced by shell fragments). One cage of 100 Virginia clams was lost in the September 1981 storm. All remaining cages containing Virginia clams were lost during a severe storm in June 1982; however, one cage containing 100 Virginia clams was found at low tide approximately 20 m north of the experimental site. All 100 clams were alive and were replanted in a new cage. Of these, 40 died during the next sampling period (June to September 1982).

Growth of the three clam stocks did vary significantly (Analysis of Co-variance [ANCOVA] $\alpha = 0.05$) over the 2-year period. Analysis of Variance with *a posterioi* multiple comparisons by Duncan procedure and Student-Newman-Keuls test (Sokal and Rohlf 1969) at the 0.05 level showed that all stocks varied significantly from one another in size at initial planting. After one year, the Virginia stock was significantly larger than the Massachusetts stock but did not vary significantly in size from the Georgia stock. The Georgia and Massachusetts stocks did not vary significantly after one year due to high within-group variation. After two years, however, the Georgia stock was significantly smaller than the Virginia stock.

The ranking of mean shell lengths changed in the first year but remained constant in the second year of growth. Georgia and Virginia clams grew from mean sizes of 10.4

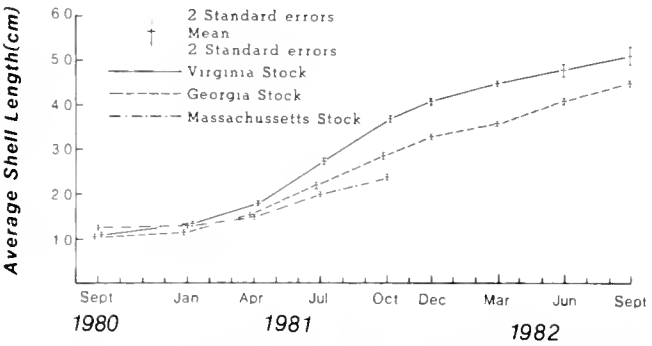


Figure 2. Growth curves in terms of shell length clam stocks from Georgia, Virginia, and Massachusetts grown in coastal waters of Georgia.

TABLE 1.

Mean survival of stocks of hard clams (*Mercenaria mercenaria*) grown on Cabbage Island, Wassaw Sound, GA, from September 1980 to September 1982.

Stock	Mean #·m^{-2} (Initial) Sep 1980	Mean # Survivors Jan 1981	Mean # Survivors Apr 1981	Mean # Survivors Jul 1981	Mean # Survivors Sep 1981	Percent Survival
Georgia	1000	874	491	387	292	29.2
Virginia	1000	714	427	388	313	31.3
Massachusetts	1000	693	525	253	143	14.3
Total	3000	2281	1443	1028	748	24.9
Stock	**Sep 1981**	**Dec 1981**	**Mar 1982**	**Jun 1982**	**Sep 1982**	
Georgia	125	102	81	80	80	64.1
Virginia	100	87	86	12.5	7.5	7.5
Massachusetts	0	-	-	-	-	0.0
Total	225	189	167	93	88	34.9

and 11.0 mm to 28.7 and 36.9 mm, respectively (Figure 2). Massachusetts clams grew from a mean initial shell length of 12.8 to 23.9 mm. Georgia, Virginia, and Massachusetts clams grew at a mean monthly rate of 1.5, 2.2, and 1.3 mm, respectively. During the second year, Georgia and Virginia clams grew from 28.7 and 36.9 mm to 45.2 and 51.6 mm, respectively. During the second year, Georgia and Virginia clams increased in shell length at a mean monthly rate of 1.4 and 1.3 mm, respectively. For the 2-year period, the Georgia and Virginia clams increased in shell length at a mean monthly rate of 1.5 and 1.7 mm, respectively. As noted above, the Massachusetts clams were lost in the second year. Growth values best fit a power curve and appropriate growth equations calculated for each stock are given in Table 2.

TABLE 2.

Growth curve equations for Georgia, Virginia, and Massachusetts clam stocks for the period September 1980 to September 1982. (Y equals shell length in mm and x equals time in months. Each N equals the mean of all clams per stock per time period.)

Stock	(N)	Growth Equation	Correlation Coefficient
Georgia	(9)	$y = 7.71 \times^{0.52}$	$r^2 = 0.8558$
Virginia	(9)	$y = 8.35 \times^{0.52}$	$r^2 = 0.8791$
Massachusetts	(5)	$y = 11.47 \times^{0.23}$	$r^2 = 0.6499$

DISCUSSION

The Virginia stock of hard clams used in this study arrived in Georgia at 11-mm length and were approximately 6 mo old. By March 1982, at 24 mo of age, 55% (N=384) of these clams were > 44.4 mm in shell length (legal size limit in Georgia). By September 1982, 90% of the Virginia clams had attained 44.4 mm. Of the unselected Georgia natural stock, 59% were > 44. 4 mm in shell length by September 1982 and 84% had attained this size by December 1982. Thirty-three months were required for the unselected Georgia clams to reach the marketable size of 44.4 mm as opposed to 24 mo for the Virginia clams. In Virginia, clams from the same hatchery, but not necessarily the same stock, were planted in the field at a size of 2 mm and grew at a rate of 1.5 mm·mo^{-1} over an 11-mo test period (Kraeuter and Castagna 1978). In another Virginia field study (Castagna and Kraeuter 1977), 2-mm clams grew to littleneck size (42 mm) in 22 to 28 mo. Clam larvae require 8 to 10 days to reach the setting stage and an additional 6 wk to attain a size of 2 mm (Castagna and Kraeuter 1977). Hence, clams in Virginia require a total of 24 to 30 mo in culture after fertilization to grow to 42 mm. Thus, clams from comparable stocks grown in different locales but under different environmental conditions required approximately the same amount of time to achieve a marketable size in both Georgia and Virginia.

The Massachusetts clams averaged 12.8 mm in length and were approximately 1 yr of age when received. No significant growth occurred after the first 3 mo of outgrowth. By September 1981, none of the Massachusetts stock had attained legal size.

The reason for the low growth rate of the Massachusetts clams is unknown but may be related to differences in ecological and/or genetic parameters between northern and southern stocks. In Massachusetts, hard clams occur primarily in subtidal areas and their growth occurs mainly in the summer (Belding 1931) whereas in Georgia, hard clams occur intertidally and grow year around. These results suggest that this Massachusetts clam stock is inadequate for growing in coastal waters of Georgia. Furthermore, clams of a 6-mm mean length from another Massachusetts hatchery were planted at the same site and in the same type of cages in 1982. Fifty-two percent of these clams, when planted at 509·m^{-2}, grew to commercial size (44. 4 mm) in 14 mo and 83% had obtained that size in 17 mo (Walker 1984b).

Clam growth in Georgia compares well with growth in other southern areas. Seed clams (mean shell length = 13 mm) that were planted at low densities (290·m^{-2}) in South Carolina reached commercial size (44 to 45 mm) after 20 mo of growout (Eldridge et al 1979). Virginia clams (mean initial length = 11 mm) that were grown in Georgia achieved the same length in 24 mo. The Georgia clams (mean initial length = 10 mm) reached commercial size in 33 mo. In Flordia, seed clams (mean shell length = 8 mm) grew to 41 in 20 mo (Menzel 1964).

The use of pens, baffles, and gravel overlay (standard and successful techniques used in Virginia by Castagna et al. [1970], Castagna and Kraeuter [1977], Kraeuter and Castagna [1978]), met with limited success in Georgia (Walker unpublished data). As seen in this experiment, gravel was quickly buried by shifting sediments. Gravel overlays used in other experiments in varying substrates (mud or sandy-mud) and areas (creeks, sandflats, or mudflats) met with similar results (Walker unpublished data). Cages and baffles that were placed in creeks were either buried by shifting sediments or washed out. Those used on mud- or sandflats were partially successful. The failure of these devices resulted from stronger tidal currents in Georgia than in Virginia's eastern shore area. The use of gravel also failed in Chesapeake Bay (Haven and Loesch 1973) and Alligator Harbor, FL (Menzel et al. 1976).

In the present study, low clam survial during the first year resulted from predation by the crabs *C. sapidus* and *P. herbstii*. Juvenile blue crabs were frequently found in the cages and shell fragments characteristic of blue crab predation (MacKenzie 1977, Krantz and Chamberlain 1978) were abundant. Crabs presumably entered as postlarvae or very small juveniles and grew, feeding on detritus and worms (Laughlin 1982). Since the cages were sampled seasonally, crabs that entered cages as postlarvae or small juveniles could grow to sufficient size to prey upon the clams. In cages that were checked monthly for crabs, > 80% clam survival

can be obtained (Walker 1984b). Juvenile crabs (either *C. sapidus* and/or *P. herbstii*) were found and removed at each sampling.

Survival is the major problem for clam mariculture in Georgia. Site selection is an important key in controlling both tidal washout and burial of cages. Cages that are placed on protected sandflats generally have less chance of burial by shifting sediments (personal observations). Cages can be constructed by attaching vexas netting to 16-mm iron reinforcing rods. Cages can be weighted to withstand tidal washout, but the problems of burial and crab predation remain. Crab predation within cages can be controlled by sieving the top centimeter of sediment at least monthly to remove newly metamorphosed crabs (Walker 1984b). Visual inspection for crabs within cages does not provide sufficient control. Cages must be checked at least montly until seed clams reach 20 mm length. Above this length clams appear to be safe from crab predation (Walker 1984b).

ACKNOWLEDGMENTS

The authors wish to thank Drs. A. C. Benke, E. Chin, J. Crenshaw, D. Gillespie, R. Mann, D. Menzel, K. R. Tenore, and two anonymous reviewers for reviewing the manuscript. Special thanks are given to Ms. A. Boyette and S. McIntosh for the graphics and to L. Land for typing the manuscript. The work was supported by the Georgia Sea Grant Program, under grant number USDL-RF/8310-21-RR100-102.

REFERENCES CITED

Ansell, A. D. 1968. The rate of growth of the hard clam, *Mercenaria mercenaria* (L.), throughout the geographical range. *J. Cons. Perm. Int. Explor. Mer.* 31:364-409.

Belding, D. L. 1931. The quahog fishery of Massachusetts. The Commonwealth of Massachusetts, Marine Fisheries, Series No. 2:41 p.

Castagna, M. & J. N. Kraeuter. 1977. *Mercenaria* culture using stone aggregate for predator selection. *Proc. Natl. Shellfish. Assoc.* 67:1-6.

Castagna, M. A., L. W. Mason & F. C. Briggs. 1970. Hard clam culture method development at VIMS. Aggregates on bottom protect seed clams from predators. *VA. Inst. Mar. Sci. Mar. Resour. Advis. Serv.* 4:3 p.

Chesnut, A. F., W. E. Fahy & H. J. Porter. 1957. Growth of young *Venus mercenaria*, *Venus campechiensis*, and their hybrids. *Proc. Natl. Shellfish. Assoc.* 47:50-56.

Eldridge, P. J., A. G. Eversole & J. M. Whetstone. 1979. Comparative survival and growth rates of hard clams, *Mercenaria mercenaria*, planted in trays subtidally and intertidally at varying densities in a South Carolina estuary. *Proc. Natl. Shellfish. Assoc.* 69:30-39.

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

Folk, R. L. 1974. *Petrology of sedimentary rocks.* Austin, TX: Hemphill Publishing Co. 184 p.

Harris, D. C. 1980. Survey of the intertidal and subtidal oyster resources of the Georgia coast. Brunswick, GA: *Georgia Dep. Natl. Resour. Coast. Resour. Div.* 44 p.

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

Haven, D. S. & J. G. Loesch. 1973. An investigation into commercial aspects of the hard clam fishing and development of commercial gear for the harvest of molluscs. Gloucester Point, VA: Mar. Sci. Ann. Contract Rep. July, 1972 through June 30, 1973; No. 3-124 R:91 p.

Kraeuter, J. N. & M. Castagna. 1978. An analysis of gravel, pens, crab traps and current baffles as protection for juvenile hard clams (*Mercenaria mercenaria*). *Proc. World Mariculture. Soc.* 8:581-592.

Krantz, G. E. & J. F. Chamberlain. 1978. Blue crab predation on cultchless oyster spat. *Proc. Natl. Shellfish. Assoc.* 68:38-42.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Applachicola Estuary, Florida. *Bull. Mar. Sci.* 32:807-822.

Loosanoff, V. L. 1939. Effects of temperature upon shell movements of clams, *Venus mercenaria* (L). *Biol. Bull. (Woods Hole)* 76:171-182.

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

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

———. 1964. Seasonal growth of northern and southern quahogs, *Mercenaria mercenaria* and *M. campechiensis*, and their hybrids in Florida. *Proc. Natl. Shellfish. Assoc.* 53:111-119.

Menzel, R. W., E. W. Cake, M. L. Haines, R. E. Martin & L. A. Olsen. 1976. Clam mariculture in northwest Florida: field study on predation. *Proc. Natl. Shellfish. Assoc.* 65:59-62.

National Marine Fisheries Service (Office of Fisheries Development). 1977. The molluscan shellfish industries and water quality: problems and opportunities. *U.S. Dep. Commer. Natl. Mar. Fish. Serv.* (Available from: Supt. Docs., U.S. Govt. Print. Off., Washington, D.C.) No.:003-020-00142-4:46 p.

Roels, O. A., K. C. Haines & J. B. Sunderlin. 1976. The potential yield of artificial upwelling mariculture. *10th European symposium on marine biology*, Ostend, Belgium. Vol. 1:381-390.

Sokal, R. R. & F. J. Rohlf. 1969. *Biometry.* San Francisco, CA: W. H. Freeman and Co. 776 p.

Walker, R. L. 1984*a*. Population dynamics of the hard clam, *Mercenaria mercenaria* (Linné) and its relation to the Georgia hard clam fishery. Atlanta, GA: Georgia Inst. of Technology. 121 p. Thesis.

———. 1984*b*. Effects of density and sampling time on growth of the hard clam, *Mercenaria mercenaria*, planted in predator-free cages in coastal Georgia. *Nautilus* 98:114-119.

———, M. A. Fleetwood & K. R. Tenore. 1980. The distribution of the hard clam, *Mercenaria mercenaria* (Linné), and clam predators in Wassaw Sound, Georgia. *GA. Mar. Sci. Cen. Tech. Rep.* 80-8:59 p.

Walker, R. L. & K. R. Tenore. 1984. The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. *Estuaries* 7:19-27.

Woodburn, K. D. 1963. Survival and growth of laboratory-reared northern clams (*Mercenaria mercenaria*) and hybrids (*M. mercenaria* X *M. campechiensis*) in Florida waters. *Proc. Natl. Shellfish. Assoc.* 52:31-36.

Journal of Shellfish Research, Vol. 4, No. 2, 131-137, 1984.

AGE AND GONAD DEVELOPMENT IN THE GEODUCK CLAM *PANOPE ABRUPTA* (CONRAD) FROM SOUTHERN BRITISH COLUMBIA, CANADA

N. A. SLOAN AND S. M. C. ROBINSON
Department of Fisheries and Oceans
Fisheries Research Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6
Canada

ABSTRACT In a southern British Columbia subtidal sandbed the deep-burrowing, Pacific geoduck clam *Panope abrupta* spawned mostly from June to July, prior to highest seawater temperature in August, 1983. Spawning was synchronous between sexes and occurs annually. Clams averaged 0.8 kg in total weight and 31.4 yr of age. Ripe gonads were found in clams ranging from 7 to 107 yr old, suggesting that individuals may be capable of reproducing over a century. Weight and dimension increases in valves and soft parts correlated significantly with age. Age, however, did not explain an appreciable amount of the residual variance in the regression of visceral mass (gonad and digestive diverticula) weight on body weight. Thus, no 'reproductive senility' occurs over the long reproductive life of *P. abrupta*. Age frequencies revealed an estimated mortality rate of 0.035 and low geoduck recruitment over at least the previous decade. Our results are compared to life history generalizations of deep-burrowing bivalves from other temperate habitats.

KEY WORDS *Panope abrupta*, geoduck clam, gametogenesis, reproduction

INTRODUCTION

The Pacific geoduck clam *Panope abrupta* (Conrad 1849) (syn. *P. generosa* Gould 1850, Bernard 1983) is a large, long-lived, and deep-burrowing hiatellid which occurs from Alaska to Baja, California (Goodwin 1973, 1976; Haderlie and Abbot 1980). It supports important diving fisheries in British Columbia (Harbo and Peacock 1983) and Washington State (Goodwin and Shaul 1984).

Harbo and Peacock (1983) reported a preliminary estimate of stock size (115,000 t) in water depths from 0 to 18.5 m along the British Columbia coast south of 51° N latitude, but this estimate excluded the population occurring in water depths of > 18.5 m. Age and size data of some natural populations and market samples and preliminary observations on predation, recruitment, mortality, and reproduction have been published (Turner and Cox 1981, Breen and Shields 1983, Harbo et al. 1983, Sloan and Robinson 1983). Nevertheless, information on the life history of *P. abrupta* in British Columbia is incomplete.

We report here on the gonadal development cycle, gonad index, age, and morphometrics of a southern British Columbia population sampled over 15 consecutive months. These findings are compared with those from Washington State (Goodwin 1973, 1976; Goodwin and Shaul 1984) and are discussed in relation to life history patterns of other deep-burrowing bivalves.

MATERIALS AND METHODS

Each month from mid-September 1982 to mid-November 1983, divers collected an average of 27 (range 20 to 32) geoduck clams from a subtidal sandbed at 12 to 15 m depth in Hammond Bay, southern British Columbia (Figure 1). Clam siphon tips or 'shows' were located and the clams were excavated using a water jet supplied by a surface pump. Between November and February few or, in some months, no 'shows' were visible and geoducks were located by probing depressions in the substrate to stimulate further siphon withdrawal. Clams were immediately taken to the laboratory where their soft portions were removed for dissection into body components (siphon, mantle muscle, foot) and the visceral mass (alimentary canal and digestive diverticula sheathed in gonadal tissue). Body components and valves were drained of excess fluid and weighed. A transverse section of the visceral mass, from the same area on the right side and including part of the surface, was removed for preservation in Davidson's fixative (with acetic acid) for histological preparation. Preserved tissue samples were embedded in paraffin within 14 days, sectioned at 5- to 6-μm intervals, stained in hematoxylin-eosin, and mounted on slides. Throughout the collecting period, daily seawater temperature was recorded on a thermograph in the Pacific Biological Station from water taken at 18 m depth in Departure Bay, located approximately 3 km south of Hammond Bay.

The right valve was measured with vernier calipers to the nearest 1.0 mm for length (Harbo et al. 1983) and hinge plate thickness (Figure 2). Ages of 365 individuals were successfully determined by the acetate peel method of Shaul and Goodwin (1982). The right valve was sectioned through the hinge plate, the cut surface polished, etched with dilute (1.0%) hydrochloric acid for 30 sec, and an acetate peel made for microscopic examination of growth rings. The hinge plate was used as it is a protected shell area which experi-

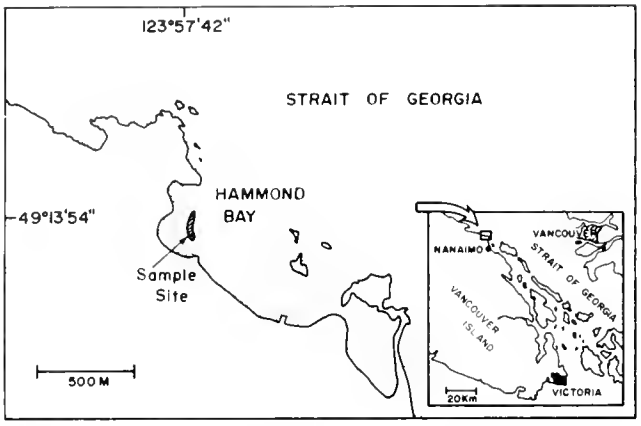


Figure 1. Location of the subtidal *Panope abrupta* sampling site in Hammond Bay, southern British Columbia.

ences no erosion (Shaul and Goodwin 1982). Each peel was counted three times to confirm the estimate of age. Shell damage during collection excluded age determinations of 39 individuals. Mortality rate was estimated from the slope of the regression of natural log of frequency on age.

Each investigator independently examined the histological sections microscopically to qualitatively assess gonadal condition. Differences in interpretation of gonadal condition were later resolved. Males and females were classified into one of five stages as described by Holland and Chew (1974), Goodwin (1976), and Mann (1982). Males have distinctive sperm ducts (Andersen 1971) which enabled sexing among spent and early active male clams. We found that geoduck ova were often elongated especially in the developing stages, a condition encountered in *Arctica islandica* (Linné) by Mann (1982). Thus, diameter measurements were not possible for calculations describing their developmental stage. A monthly gonadal index was calculated from measurements of the weight of the visceral mass (gonad and digestive diverticula) relative to the total weight (without valves).

RESULTS

Sex ratio, mophometrics, and age

Table 1 lists the weight and age characteristics of the 229 males (56.7%) and 175 females (43.3%) of *P. abrupta*. No hermaphroditic geoducks were found. Females were slightly larger (maximum total weight = 1.42 kg) and older than males. The relative proportion of weight represented by the different body components were similar for each sex. Geoducks averaged 31.1 yr old and ranged in age between 4 to 107 yr. The proportion of males of *P. abrupta* decreased steadily from a high of 90% of all individuals ≤ 10 yr-old to 47% of geoducks ≥ 51 yr-old (Figure 3).

The age-frequency histogram in Figure 4 shows that the 21- to 30-yr-old group was modal. Numbers of clams between ages of 11 and 20 yr were lower than expected.

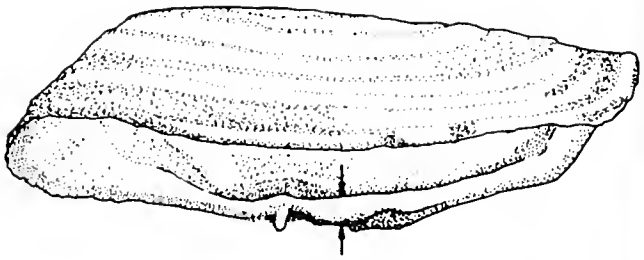


Figure 2. Site of the hinge plate thickness measurement from a valve of *Panope abrupta*.

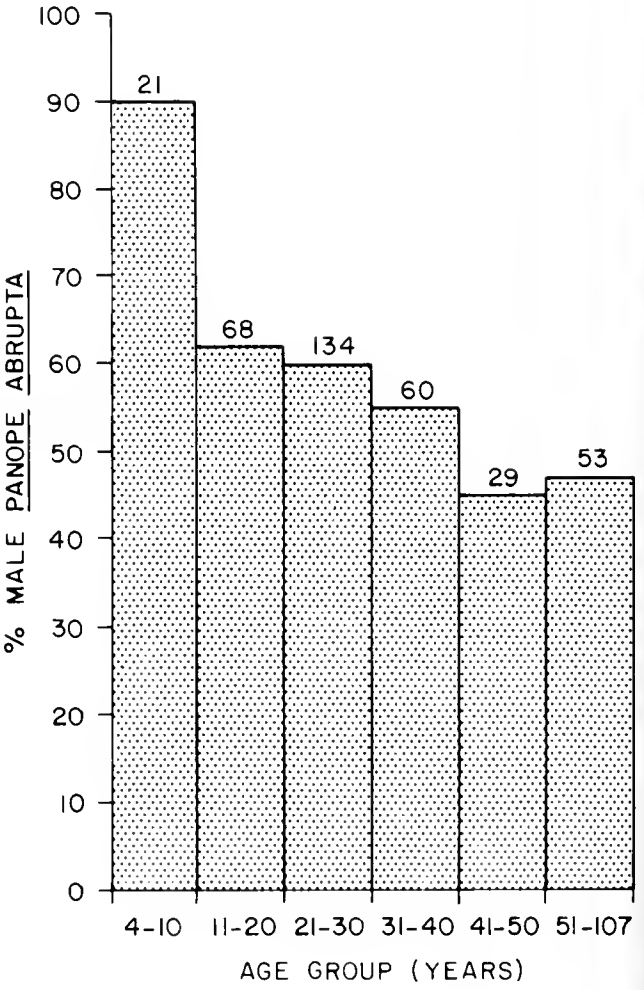


Figure 3. Histogram demonstrating percent of males of *Panope abrupta* according to age group. Numbers at the column tops are total numbers of clams in each age group.

Estimated mortality rate from the total sample (n = 365) was 0.035. Mortality rate of all clams subsequent to the period of high recruitment, i.e., ≥ 21 yr old (n = 276), was 0.054.

The correlation coefficients in Table 2 demonstrate that valve weight and hinge-plate thickness correlated better with age than body weight and valve length did with age. Visceral mass weight was least strongly correlated with age.

TABLE 1.
Differences in biomass and age between males and females of *Panope abrupta* from southern British Columbia.

	Weight characteristics						Age characteristics		
		Total weight (g)		Mean % of total weight according to portion				Years	
Sex	n	$\bar{x} \pm SD$	Range	Valve	Body	Visceral mass	n	$\bar{x}$	Range
Male	229	773.1 ± 232.9	55.5 −1352.5	21.4	69.0	9.6	213	29.3	4-107
Female	175	841.9 ± 199.6	204.0 −1421.7	22.6	67.6	9.8	152	34.3	6-89
Total	404	802.9 ± 221.5	55.5 −1421.7	21.9	68.4	9.7	365	31.4	4-107

TABLE 2.
Regression formulae of *Panope abrupta* age versus valve and weight characteristics. All relationships are described by the allometric relationship: $y = ax^b$.

Regression equation	n	r
Age = 0.372·valve weight $^{0.85}$	365	0.79*
Age = 0.340·hinge plate thickness $^{2.11}$	365	0.77*
Age = 0.141·body weight $^{0.83}$	365	0.57*
Age = 9.7 x 10^{-5}·valve length $^{2.52}$	365	0.56*
Age = 4.096·visceral mass weight $^{0.44}$	365	0.35*

*Significance ($p<0.05$).

To examine whether older clams achieve less reproductively, we analyzed how much of the residual variance around the linear regression of log reproductive effort (visceral mass weight of ripe clams) on log body weight was explained by age. Only ripe clams were used because their gonadal development was maximal. The multiple regressions, converted to power curve formulae in Table 3, show that the age variable explained <0.8% of the total variance in the relationship between visceral mass weight versus body weight and age combined, in either males or females.

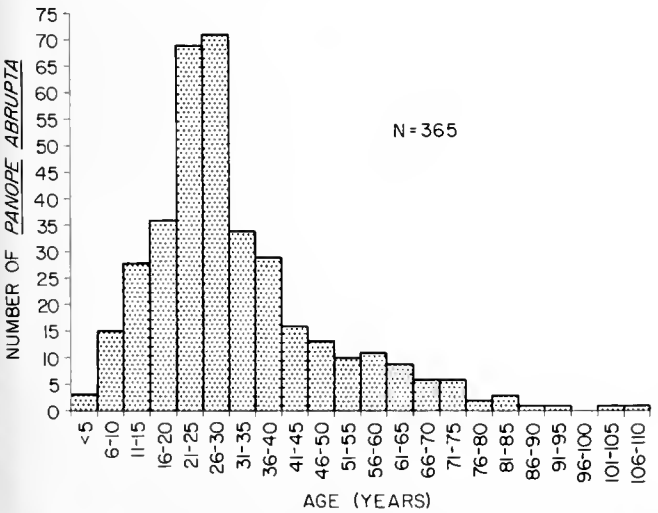


Figure 4. Histogram of age frequencies of the *Panope abrupta* sample.

Reproduction

The reproductive cycles of males and females of *P. abrupta* are illustrated in Figure 5 along with the mean weekly seawater temperature. As the seawater temperature decreased in the autumn most geoducks, of both sexes, developed from early-active to late-active gametogenic stages. Most clams were ripe in April and May, but synchronization of ripeness among females was greater than among males. Most spawning, as indicated by the partially spent condition, occurred between June and July, although spawning was a more protracted event among males (April to November) than females (June to August). In the warmest month, August, gonad recovery and the reinitiation of gametogenesis occurred, especially among females. As the autumn progressed, gonadal development became more active in preparation for spawning in the forthcoming warm season.

The mean gonadal index reflected the spawning cycle (Figure 6). Maximum visceral mass weight occurred during the late-active to ripe stages. The marked April decrease, followed by recovery in both male and female indexes, is attributed to an artifact in the data. Most appropriately, spawning in June and July coincided with a marked decline of the gonadal index, followed by an increase in the index.

Unequivocally mature geoducks were 6 to 103 yr old and 12 to 95 yr old for late-active males and females, respectively. The ages of ripe individuals ranged from 7 to 107 yr and 8 to 89 yr for males and females, respectively. Photomicrographs illustrate gonadal development in the youngest late-active male and the ripe stage in the oldest male and youngest and oldest female geoducks (Figures 7 to 10). The reproductive status of all old ($\geq$ 50 yr) geoducks demonstrated that they were reproductively active (Table 4).

DISCUSSION

The June to July spawning peak observed for *Panope abrupta* agreed with findings for Washington State populations (Andersen 1971; Goodwin 1973, 1976) and prelim-

TABLE 3.
Multiple regression formulae of visceral mass weight (VMW), of ripe geoduck clams only, versus body weight (BW) and age.

Sex	n	Multiple regression equation	Variable	SS	contribution to SS	r^2
Male	36	$VMW = 0.2254 \cdot BW^{0.944} \cdot Age^{-0.051}$	BW	1.8938	99.2	0.42
			Age	0.0160	0.8	
Female	27	$VMW = 1.0305 \cdot BW^{0.736} \cdot Age^{0.0054}$	BW	1.0567	99.9	0.41
			Age	0.0002	0.1	
Total	63	$VMW = 0.6650 \cdot BW^{0.785} \cdot Age^{-0.0014}$	BW	3.3023	100	0.35
			Age	0.0001	0.0	

inary observations from British Columbia (Turner and Cox 1981). Spawning probably occurs annually and is synchronous between sexes. The less concise seasonal reproductive pattern among males compared to that of females was also observed by Goodwin (1976). Other northeastern Pacific bivalves display a similar summer spawning peak, associated with high water temperatures (Porter 1974; Bourne 1979, 1982; Robinson and Breese 1982). Spawning in *P. abrupta* may be in response to changes (increases) in ambient seawater temperature, as it is for some other temperate bivalve species (Brousseau 1978, Taylor and Capuzzo 1983).

The gonadal index reflected changes in the reproductive cycle as it does in other bivalves (Feder et al. 1979). Overwintering clams had withdrawn into the substrate, but were undergoing gametogenesis by converting stored reserves. This was seen in histological preparations and in the gonadal index. The minor autumn increase in the index may have been related to feeding on an autumn plankton bloom. This increase only temporarily modified the overall trend of declining index until the onset of gametogenesis in winter.

TABLE 4.
Gametogenic states of old (≥50 years) males and females of *Panope abrupta*.

Sex	Number of *Panope abrupta* according to stage of development				
	Early Active	Late Active	Ripe	Partially Spent	Spent
Male	3	10	7	2	4
Female	15	6	5	0	2
Total	18	16	12	2	6

The male-to-female sex ratio of *P. abrupta* (57:43) was similar to that reported by Goodwin (1976) (53:47). The

TABLE 5.
Some size, age, recruitment, and mortality characteristics of deep-burrowing clams from different habitats.

Species	Habitat	Burrowing depth (cm)	Valve length maxima (cm)	Biomass maxima (kg)	Life span (yr)	Recruitment	Adult mortality	Reference
Mya arenaria	intertidal	30	10	<0.25	8	wide interannual fluctuation	can be catastrophic (hot summers)	Brousseau (1978); Goshima (1982); Pacific Biological Station, Nanaimo, B.C., Canada; N. Bourne (pers. comm.)
Tresus capax	intertidal/ shallow subtidal	60	15	<1.0	16	usually low but can fluctuate widely	low but large scale mortalities can occur	Wendell et al. (1976); Breed-Willeke & Hancock (1980); N. Bourne (pers. comm.)
Panope abrupta	subtidal*	100	20	4.5	146	low but can fluctuate	consistently low	Goodwin (1973, 1976); Breen & Shields (1983); Harbo et al. (1983); Goodwin & Shaul (1984)

**Panope abrupta* can occur in the intertidal (Andersen 1971), but only subtidal population characteristics are cited here.

higher proportions of males in the younger age classes agreed with Andersen's (1971) finding of 94.4% males among geoducks with shells < 100 mm long. Andersen (1971) and Goodwin (1976) have suggested the gonochoristic nature of geoducks, i.e., sex is determined by development and males mature at a smaller size (earlier age) than females. The possibility of some level of sex reversal and protandric hermaphroditism should be examined further.

Geoducks reproduce for over at least a 100-yr period. They mature at 5 yr of age, may live to 146 yr and experience low levels of adult mortality (Breen and Shields 1983, Harbo et al. 1983, Goodwin and Shaul 1984). The estimated mortality rate of 0.035 for the entire aged sample is higher than the maximum value of 0.019 calculated by Breen and Shields (1983).

All of the geoducks (50 to 107 yr) contained morphologically viable sperm or ova which indicated no cessation of breeding with age. Moreover, the reproductive output (visceral mass weight) of geoducks increased slightly with age as it related to body size, which itself increased with age. Despite their great age, geoducks showed no 'reproductive senility' (*sensu* Peterson 1983) or lower reproductive output than expected from the allometric (power) curve that related body size to reproductive effort among younger adults. Body weight contributed > 99.0% to variability in visceral mass weight, whereas age contributed < 1.0%.

As geoducks age, their valves gradually become thicker and heavier. The less marked increase in weight of soft parts and valve length with age was consistent with the widespread belief that geoduck body growth slows greatly by age 10 and is extremely slow thereafter (Goodwin 1973, Harbo et

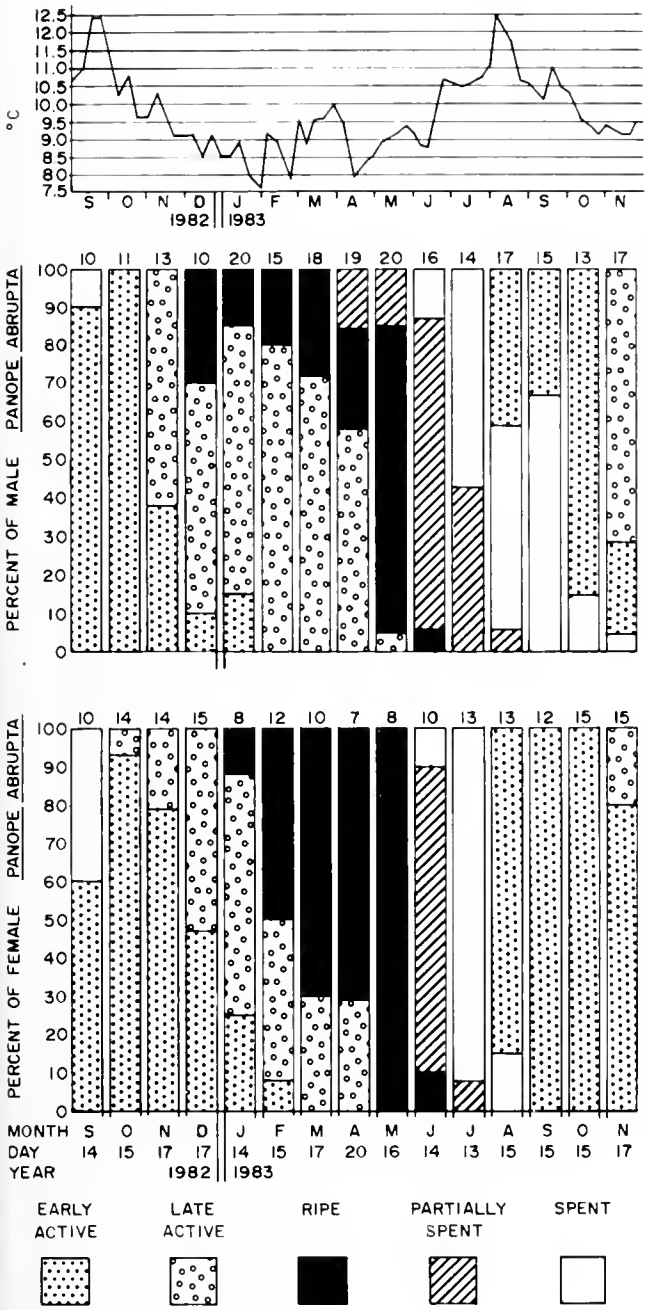


Figure 5. Gonad development cycle, illustrated as percentage of males or females of *Panope abrupta* from southern British Columbia according to development stage, from mid-September, 1982 to mid-November, 1983. Numbers at the column tops are total numbers of males or females in that month. Mean daily seawater temperature, calculated each week, from 18 m depth in Departure Bay, is provided at the top.

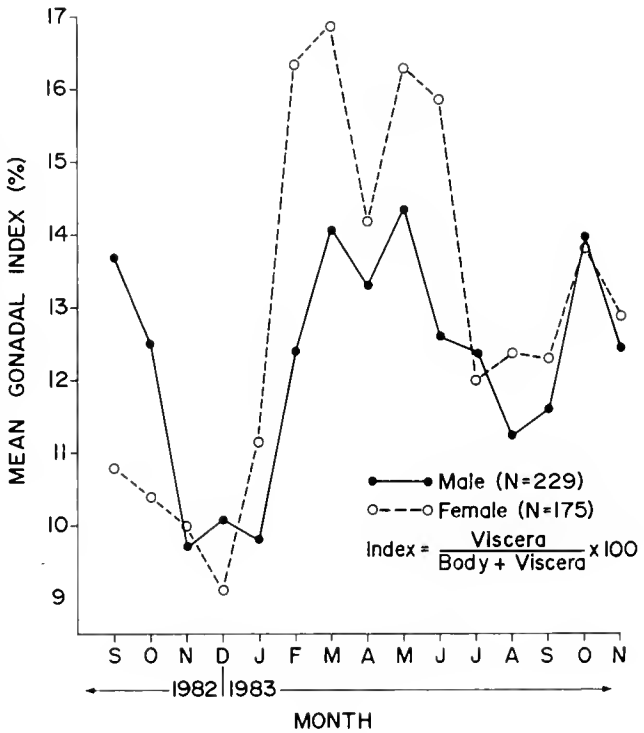
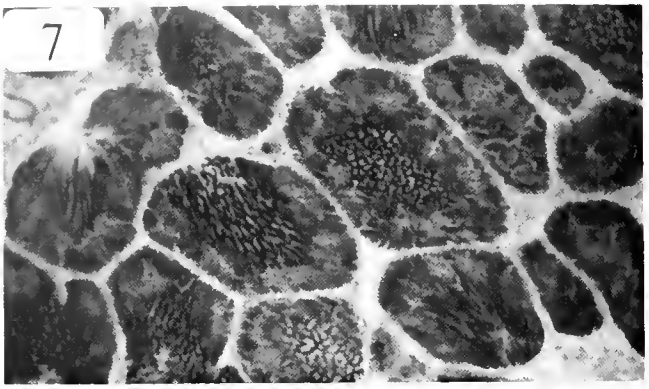
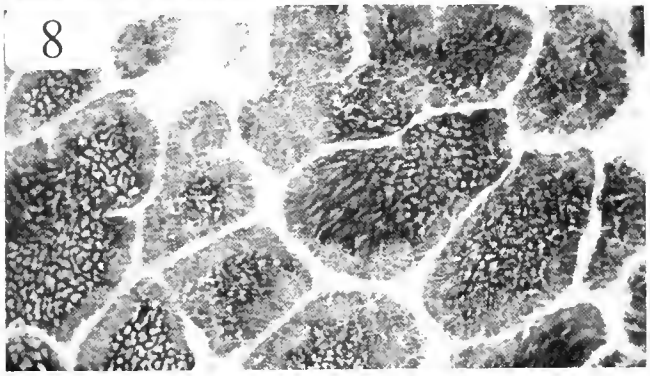
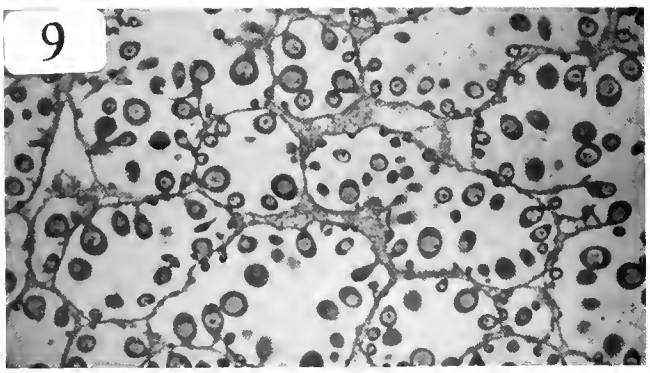
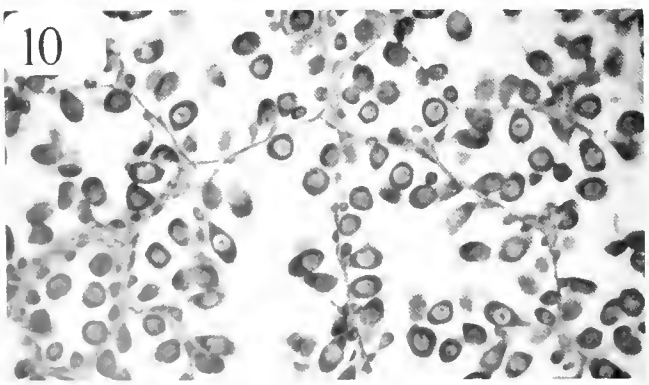


Figure 6. Mean gonadal index of males and females of *Panope abrupta* from mid-September, 1982 to mid-November, 1983. Body = siphon, mantle muscle, and foot; 'Viscera' = visceral mass of digestive diverticula sheathed in gonadal tissue.









Figures 7 - 10. Photomicrographs of cross sections of male and female gonadal tissue from individuals at the extremes of the sampled age ranges.
(7) Testis of a 106-yr-old late-active male (100x).
(8) Testis of a 107-yr-old ripe male (100x).
(9) Ovaries of an 8-yr-old ripe female (100x).
(10) Ovaries of an 89-yr-old ripe female (100x).

al. 1983, Goodwin and Shaul 1984). Valve-length increase in another long-lived clam, *Arctica islandica*, slows greatly at 20 to 30 yr of age in their 225-yr life span (Murawski et al. 1982, Sager and Sammler 1983, Ropes 1984). In contrast, three species of shorter-lived clams (< 16 yr) demonstrate more uniformly increasing valve length throughout their lives (Feder et al. 1976, Paul et al. 1976*a*, *b*).

Despite the reproductive output of so many large clams, recruitment in *P. abrupta* is low and juveniles are scarce (Breen and Shields 1983, Sloan and Robinson 1983, Goodwin and Shaul 1984). The relatively low proportion of 11- to 20-yr-old geoducks may indicate poor recruitment during at least the previous 10 yr. A similar decline in geoduck recruitment has occurred in other British Columbia localities (Breen and Shields 1983, Harbo et al. 1983) (Figure 4). Sampling bias is not likely to have influenced low numbers of 11- to 20-yr-old clams as near full valve length (and most adult body size) is reached by age 10 to 12 yr (Goodwin 1973). Similarly, fishermen tend to miss only geoducks < 12 yr-old as revealed by market samples (Harbo et al. 1983).

Wholly buried (winter season) geoducks participate in a seasonally synchronized reproductive cycle. We did not, however, sample buried geoducks during the other seasons as sufficient clams were 'showing' to permit complete sample collection. Given that the maximum 'show' factor approached 80-90% of the population (Goodwin 1973, 1977; Lynn Goodwin, Washington Dept. of Fisheries, Brinnon, WA, pers. comm.), a proportion of the clam population remained buried, even during times of optimal feeding conditions such as the spring plankton bloom. Warm season withdrawal was probably for only short periods (L. Goodwin, pers. comm.).

Life history characteristics of *P. abrupta* were compared with the deep-burrowing *Mya arenaria* (Linné) and *Tresus capax* (Gould) from different temperate habitats (Table 5). All grew rapidly in early, postsettlement life to attain sufficient size and thus the shelter of deep sediment depth. That refuge of depth apparently led to greatly decreased adult mortality. Moreover, the adults, none of which was fully encased by its valves, lost the ability to rebury themselves if removed from the sediment. In all three species the end of the rapid burrowing stage coincided with, or was soon followed by, the beginning of annual reproductive activity. Of these deep-burrowing clams, *P. abrupta* occupied the physically more stable (subtidal) habitat, was long-lived, and had generally low recruitment and low adult mortality rates. The other species occured in physically less predictable environments and experienced fluctuations in recruitment and adult mortality. This may relate to their occupation of the intertidal zone and habit of shallower burrowing.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge J. W. Bagshaw for the histological preparations, G. S. Jamieson for support through this study, and L. Goodwin and P. A. Breen for

advice and encouragement. Lesa Pomeroy aged the samples, M. D. Wells sectioned the valves, S. Greenham drafted the figures, and numerous tenders aided throughout our diving schedule. Neil Bourne, P. A. Breen, D. Fyfe, L. Goodwin, G. S. Jamieson, and D. O'Foighil commented on early drafts.

REFERENCES CITED

Andersen, A. M. 1971. Spawning, growth and spatial distribution of the geoduck clam, *Panope generosa* Gould in Hood Canal, Washington. Seattle, WA: Univ. of Washington; Available from: University Microfilms, Ann Arbor, MI; Publ. No. 72-07315. 145 p. Dissertation.

Bernard, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. *Can. Spec. Publ. Fish. Aquat. Sci.* 61:102 p.

Bourne, N. 1979. Razor clam, *Siliqua patula* Dixon, breeding and recruitment at Masset, British Columbia. *Proc. Natl. Shellfish. Assoc.* 69:21-29.

_____ . 1982. Distribution; reproduction, and growth of Manila clams, *Tapes philippinarum* (Adams and Reeves), in British Columbia. *J. Shellfish Res.* 2:47-54.

Breed-Willeke, G. M. & D. R. Hancock. 1980. Growth and reproduction of subtidal and intertidal populations of the gaper clam *Tresus capax* (Gould) from Yaquina Bay, Oregon. *Proc. Natl. Shellfish. Assoc.* 70:1-13.

Breen, P. A. & T. L. Shields. 1983. Age and size structure in five populations of geoduck clams (*Panope generosa*) in British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* 1169:62 p.

Brousseau, D. J. 1978. Spawning cycle, fecundity, and recruitment in a population of soft-shell clams, *Mya arenaria*, from Cape Ann, Massachusetts. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.* 76:155-166.

Feder, H. M., J. C. Hendee, P. Holmes, G. J. Mueller & A. J. Paul. 1979. Examination of a reproductive cycle of *Protothaca staminea* using histology, wet weight-dry weight ratios, and condition indices. *Veliger* 22:182-187.

Feder, H. M., A. J. Paul & J. Paul. 1976. Growth and size-weight relationships of the pinkneck clam *Spisula polynyma*, in Hartney Bay, Prince William Sound, Alaska. *Proc. Natl. Shellfish. Assoc.* 66:21-25.

Goodwin, L. 1973. Subtidal geoducks of Puget Sound, Washington. *Wash. Dep. Fish. Tech. Rep.* 13:64 p.

_____ . 1976. Observations on spawning and growth of subtidal geoducks (*Panope generosa*, Gould). *Proc. Natl. Shellfish. Assoc.* 65:49-58.

_____ . 1977. The effect of season on visual and photographic assessment of subtidal geoduck clam (*Panope generosa* Gould) populations. *Veliger* 20:155-158.

_____ & W. Shaul. 1984. Age, recruitment and growth of the geoduck clam (*Panope generosa* Gould) in Puget Sound, Washington. *Wash. Dep. Fish. Tech. Rep.* 215:30 p.

Goshima, S. 1982. Population dynamics of the soft-clam, *Mya arenaria* L., with special reference to its life history pattern. *Publ. Amakusa Mar. Biol. Lab. Kyushu Univ.* 6:119-165.

Haderlie, E. C. & D. P. Abbott. 1980. Bivalvia: The clams and allies. Morris, R. H., Abbott, D. P., & Haderlie, E. C., eds. *Intertidal invertebrates of California*, Stanford, CA: Stanford Univ. Press. 355-411.

Harbo, R. M., B. E. Adkins, P. A. Breen & K. L. Hobbs. 1983. Age and size in market samples of geoduck clams (*Panope generosa*). *Can. Manuscr. Rep. Fish. Aquat. Sci.* 1714:77 p.

Harbo, R. M. & S. D. Peacock. 1983. The commercial geoduck clam fishery in British Columbia, 1976 to 1981. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 1712:40 p.

Holland, D. A. & K. K. Chew. 1974. Reproductive cycle of the manila clam (*Venerupis japonica*) from Hood Canal, Washington. *Proc. Natl. Shellfish. Assoc.* 64:53-58.

Mann, R. 1982. The seasonal cycle of gonadal development in *Arctica islandica* from the southern New England shelf. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.* 80:315-326.

Murawski, S. A., J. W. Ropes & F. M. Serchuk. 1982. Growth of the ocean quahog, *Arctica islandica*, in the middle Atlantic Bight. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.* 80:21-34.

Paul, A. J., J. M. Paul & H. M. Feder. 1976*a*. Growth of the littleneck clam, *Protothaca staminea*, on Porpoise Island, southeast Alaska. *Veliger* 19:163-166.

_____ . 1976*b*. Age, growth and recruitment of the butter clam, *Saxidomus gigantea*, on Porpoise Island, southeast Alaska. *Proc. Natl. Shellfish. Assoc.* 66:1-3.

Peterson, C. H. 1983. A concept of quantitative reproductive senility: Application to the hard clam, *Mercenaria mercenaria* (L.). *Oecologia (Berl.)* 58:164-168.

Porter, R. G. 1974. Reproductive cycle of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Washington. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.* 72:648-656.

Robinson, A. M. & W. P. Breese. 1982. The spawning season of four species of clams in Oregon. *J. Shellfish Res.* 2:55-57.

Ropes, J. W. 1984. Procedures for preparing acetate peels and evidence validating the annual periodicity of growth lines formed in the shells of ocean quahogs, *Arctica islandica*. *U. S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 46(2):27-35.

Sager, G. & R. Sammler. 1983. Mathematical investigations into the longevity of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Int. Rev. Gesamten Hydrobiol.* 68:113-120.

Shaul, W. & L. Goodwin. 1982. Geoduck (*Panope generosa*: Bivalvia) age as determined by internal growth lines in the shell. *Can. J. Fish. Aquat. Sci.* 39:632-636.

Sloan, N. A. & S. M. C. Robinson. 1983. Winter feeding by asteroids on a subtidal sandbed in British Columbia. *Ophelia* 22:125-141.

Taylor, R. E. & J. M. Capuzzo. 1983. The reproductive cycle of the Bay scallop, *Argopecten irradians irradians* (Lamarck), in a small coastal embayment on Cape Cod, Massachusetts. *Estuaries* 6:431-435.

Turner, K. C. & R. K. Cox. 1981. Seasonal reproductive cycle and show factor variation of the geoduck clam *Panope generosa* Gould in British Columbia. *J. Shellfish Res.* 1:125 (Abstract).

Wendell, F., J. D. Demartini, P. Dinnel & J. Siecki. 1976. The ecology of the gaper of horse clam, *Tresus capax* (Gould 1850) (Bivalvia: Mactridae), in Humboldt Bay, California. *Calif. Fish Game* 62:41-42.

Journal of Shellfish Research, Vol. 4, No. 2, 139-143, 1984.

FORAGING TACTICS OF SEVERAL CRUSTACEAN SPECIES FOR INFAUNAL PREY[1]

PETER J. AUSTER AND LEE R. CROCKETT
NOAA's National Undersea Research Program
and
Marine Sciences Institute
The University of Connecticut at Avery Point
Groton, Connecticut 06340

ABSTRACT Direct underwater observations of decapod crustaceans that were associated with infaunal bivalve assemblages revealed that they can forage for infaunal prey using a lateral burrow excavation behavior. *Cancer borealis*, *Carcinus maenas*, and *Pagurus longicarpus* are primary excavators. Activity of these species attracts secondary excavators which also forage for prey within the burrow.

KEY WORDS: foraging, behavior, crustaceans, burrowing, infaunal prey.

INTRODUCTION

The role of crustacean predators in structuring infaunal assemblages (bivalve mollusc populations in particular) and how crustaceans handle prey, have been well documented (Pratt and Campbell 1956, Virnstein 1976, MacKenzie 1977, Blundon and Kennedy 1982, Möller and Rosenberg 1983, Boulding 1984, Boulding and Hay 1984, and many others). While those studies focused on the effects of predators on prey populations and on prey handling, few have actually examined the behavioral tactics used by predators in prey location. Knowledge of foraging tactics in predator-prey relationships may help to elucidate why certain prey species are taken. In this paper, we describe aspects of the foraging behavior of several species of decapod crustaceans that are associated with infaunal bivalve assemblages in eastern Long Island Sound.

METHODS AND STUDY AREA

Direct underwater observations of decapod foraging behaviors were made opportunistically during 172 dives over shellfish beds in eastern Long Island Sound during all seasons between 1981 and 1984. Data acquisition consisted of immediate postdive debriefings, use of underwater notes, and photodocumentation of selected behaviors. Animal sizes, when noted, were measured *in situ* with a vernier caliper to the nearest 0.1 mm.

Observations were made primarily at West Harbor, Fishers Island, NY; Poquonock River Estuary, Groton, CT; and Ellis Reef, Fishers Island Sound, CT (Figure 1). The West Harbor and Poquonock River sites consisted of sublittoral, coarse-to-fine sand (flats) and stands of the eel grass *Zostera marina* L. that contained populations of the northern hard clam *Mercenaria mercenaria* (Linné) and the northern bay scallop *Argopecten irradians* (Lamarck). Water depths ranged from approximately 0.5 to 4 m. The Ellis Reef site is relatively deep (3 to 15 m) with a sloping, sandy silt substrate. *Mercenaria mercenaria* is part of the bivalve assemblage at this site also.

OBSERVATIONS

A lateral excavation foraging tactic for location of infaunal prey items was observed for the Jonah crab *Cancer borealis* Stimpson, the green crab *Carcinus maenas* (Linnaeus), and small hermit crab *Pagurus longicarpus* Say (Figure 2A, B, C). The excavations are defined as burrows or pits dug vertically into the substrate, then excavated laterally along burrow sides for the apparent purpose of exposing potential prey items. This tactic is a continuation of the dactyl probing and prey removal tactic during which predators locate single or multiple prey items and vertically excavate them from the substrate (sensu Blundon and Kennedy 1982, p. 57). These excavations do not include burrows created for protection from currents, wave surge, predators, overwintering, etc. While it was impossible to measure every individual, approximate sizes for each species which exhibited this behavior are: Jonah crab, 44.2 to 135.5 mm, carapace width; green crab, to 52.7 mm, carapace width; and small hermit crab, to 5.1 mm, length of anterior shield. In general, all size classes of each species observed in the study area exhibited this behavior during some observation period.

The excavations of these species had a similar form. Excavations were begun by using chelae and forward walking legs to scrape away surficial sediments to form a depression. A leading edge was initiated by collapsing cohesive sediments with chelae or walking legs from a side of the pit. During the entire process, material was worked through with

[1]Contribution Number 181 of The University of Connecticut, Marine Research Laboratory, Noank, Connecticut

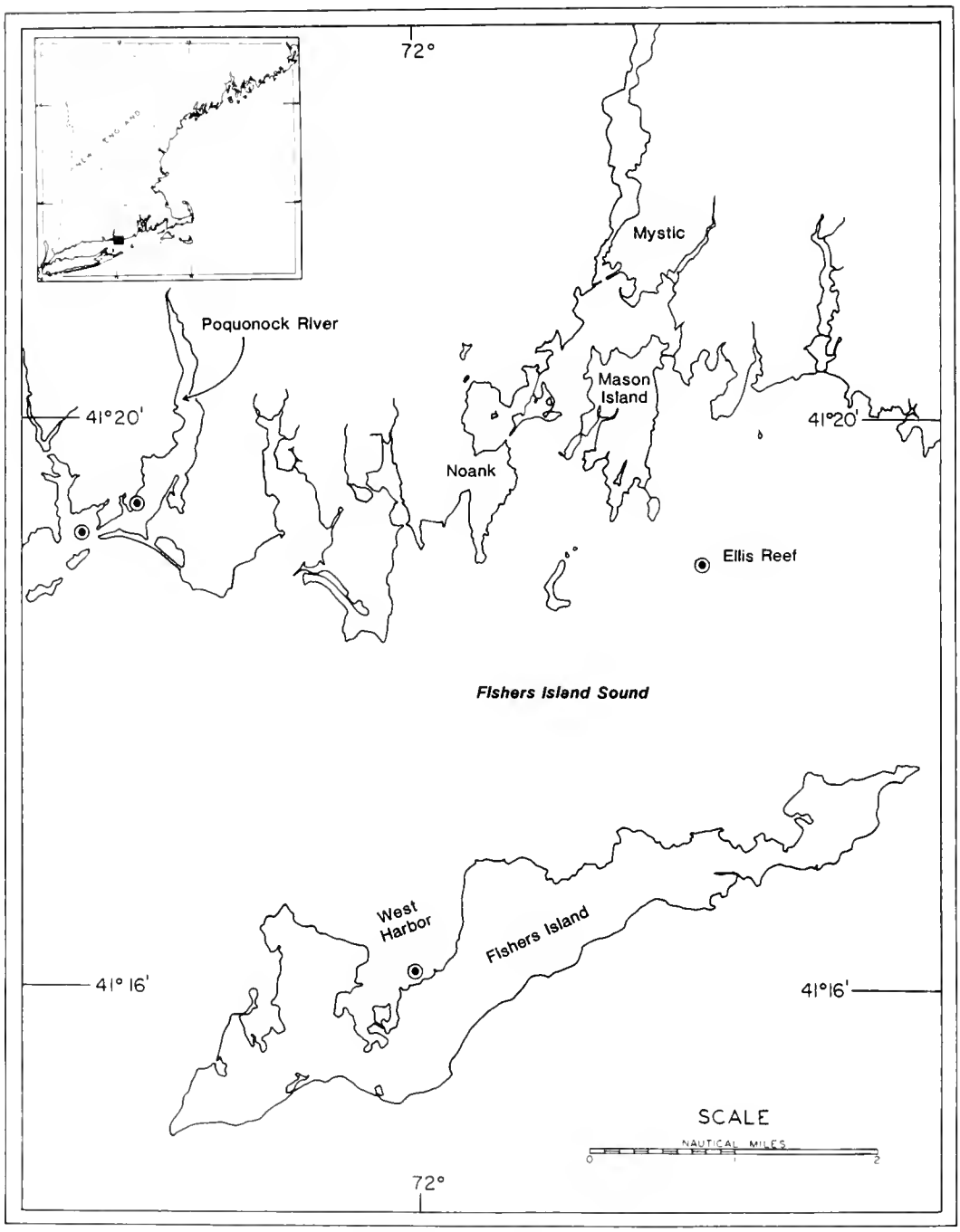


Figure 1. Locations of the study sites in Fishers Island Sound.

chelae and mandibles, selected prey items (e.g., bivalves, nereid and tubiculous polychaetes) were captured and fed upon, and sediments were plowed towards a trailing edge. The leading edge was upstream and trailing edge downcurrent in areas of high current velocity, so that excavated material was transported from the leading edge.

Each species exhibited several body orientations towards the leading edge of the excavation. In most instances, the anterior appendages were oriented towards the leading edge, and the crab worked through the sediments with one or both chelae. A side orientation was observed in which the crabs used one chela and their walking legs to collapse sediment from the leading edge of the excavation. A posterior orientation also was observed in which the rear walking legs collapsed the sediments and plowed them forward to the chelae and mandibles to be searched for potential prey.

Excavations also occurred adjacent to in-sediment structures (e.g., worm tubes, roots of *Z. marina*). The use of these supporting structures within the excavations (Figure 2D) allowed burrowing and searching to depths greater than

the sediment's unsupported angle of repose. Small hermit crabs and green crabs dug this type of excavation.

Primary excavators attracted other predatory species including sand shrimp (*Crangon septemspinosa* Say), winter flounders (*Pseudopleuronectes americanus* [Walbaum]), small hermit crabs, large hermit crabs (*P. pollicaris* Say), mud crabs (*Panopeus* spp.), and killifish (*Fundulus* spp.), that consumed prey that was not obvious to or a type or size not selected by the primary excavator. These species searched through sediments that were previously handled by the primary excavator, or they remained near the leading edge ready to capture exposed prey species. Secondary excavators and associated species were also observed in burrows abandoned by the primary excavator.

Sand shrimp (up to 52.3 mm, total length) were the most numerous and consistent of the associated predators (Figure 2E). Individuals were observed in all areas of excavations, and their activities including picking, fanning, and burrowing into the sedimentary material. Sediment and associated organisms were worked through the mandibles and appropriate prey was consumed (i.e., bivalve species less than approximately 1 mm in length).

Juvenile winter flounders (< 20 cm, total length) were occasionally seen along the peripheral areas of the excavations. The flounders preyed on exposed polychaetes, bivalves, and on small sand shrimp that also were feeding at the excavation sites.

Both small and large hermit crabs were observed to be secondary excavators when green crabs and Jonah crabs were actively digging. Mud crabs and killifish occasionally were observed picking at exposed prey items at active excavations at the two shallow sites.

Excavations by more than one green crab occasionally were noted. Up to nine green crabs were counted in an unusually large excavation with individual crabs working different edges around a large pit. Displacement of individual green crabs by larger or dominant individuals occasionally occurred.

Most individuals of all predatory species abandoned active excavations if disturbed by other organisms, such as other potential predators, and did not return. The several individuals that were observed after abandoning an excavation used their dactyls to probe the sediment surface over wider areas for prey. None was observed to return to the abandoned excavation.

Over the course of several tidal cycles, the edges of abandoned excavations eroded and became indistinguishable from the general small-scale topography of an area. Abandoned excavations occasionally were very abundant over the study areas. On 3 August 1983, a particularly active day for excavating at the Fishers Island site, 45 separate excavations were counted along a 30 m by 1 m path.

DISCUSSION

The digging behavior of decapod crustaceans has been referred to in previous studies. Virnstein (1976) discussed the effects of "tube or burrow disruption caused by digging activities associated with feeding" by the blue crab *Callinectes sapidus* Rathbun on the benthos. Turner (1948) described this same type of "digging" for blue crabs and green crabs. Gotshall (1977) noted that the Dungeness crab *Cancer magister* Dana dug 30-cm deep pits to excavate large bivalves. None of these studies described changes in foraging tactics within an excavation for any of the species discussed.

The lateral excavation behavior seems to be a continuation of the vertical dactyl probing and prey removal tactics. That is, a pit is initially excavated vertically and foraging is continued laterally along the side(s) of the pit. The cues which induce the lateral excavation tactic were not obvious during this study. A logical scenario, however, may be that foraging in an area is initially a dactyl probing activity until a prey population of some critical density is located or prey of sufficient size requires a pit type excavation. If prey continue to be located along the edge of a pit, excavating and foraging continues laterally.

The type of foraging tactic may affect probabilities of mortality. The dactyl probing and vertical excavation strategy was apparently random within a given population (area) of prey, hence the probability of survival for an individual prey organism increases at low densities (Malinowski and Whitlatch in press). The lateral excavation strategy was apparently thorough within the area of excavation and the probability of survival of an exposed individual of a proper size during the process may well be near zero.

Secondary excavators and associated organisms cue on the activity of the primary excavator and forage for prey items in the same area. The attraction of secondary predators also occurs in fish assemblages (Hobson 1968, Fishelson 1977). Individual fish that forage and feed on local prey may expose other prey items during these activities. It is beneficial for other predators to cue on individuals that exhibit foraging behaviors in order to expend less energy foraging for concealed prey items and locating local prey populations.

Crustacean excavations are ephemeral structures. Animals generally did not defend excavations and readily abandoned an area to a larger or dominant individual. The intensity of excavating was variable, although there was no readily apparent environmental cue to discern any rhythmicity in this activity.

ACKNOWLEDGMENTS

We thank Stephen Tettelbach, Robert Whitlatch, and Ed Cake for critically reviewing the manuscript, Eleanor Minikowski and Constance Fontaine for typing the various drafts of this paper, and Kurt Buchholz and Mary Jane Spring for preparing the figures. The boat crew and staff of The University of Connecticut, Marine Research Laboratory, provided indispensable ship and facilities support. This study was supported, in part, by Sea Grant funds (Grant No. NA82AA-D-00018, Project No. R/SR-1) to Robert Whitlatch.

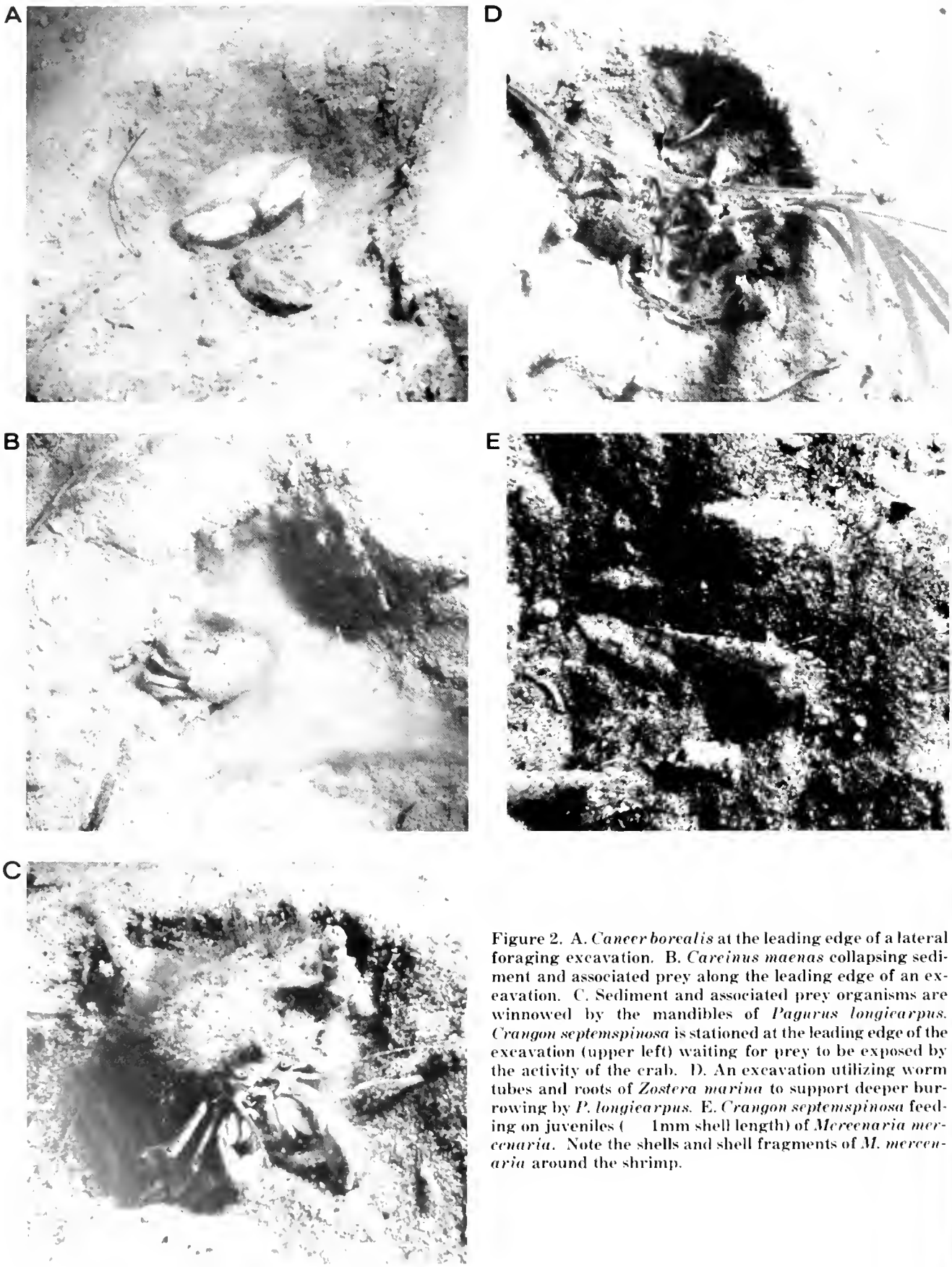


Figure 2. A. *Cancer borealis* at the leading edge of a lateral foraging excavation. B. *Carcinus maenas* collapsing sediment and associated prey along the leading edge of an excavation. C. Sediment and associated prey organisms are winnowed by the mandibles of *Pagurus longicarpus*. *Crangon septemspinosa* is stationed at the leading edge of the excavation (upper left) waiting for prey to be exposed by the activity of the crab. D. An excavation utilizing worm tubes and roots of *Zostera marina* to support deeper burrowing by *P. longicarpus*. E. *Crangon septemspinosa* feeding on juveniles (1mm shell length) of *Mercenaria mercenaria*. Note the shells and shell fragments of *M. mercenaria* around the shrimp.

REFERENCES CITED

Blundon, J. A. & V. S. Kennedy. 1982. Mechanical and behavioral aspects of the blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. Exp. Mar. Biol. Ecol.* 65:47-65.

Boulding, E. G. 1984. Crab resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* 76:201-223.

_____ & T. K. Hay. 1984. Crab response to prey density can result in density-dependent mortality of clams. *Can. J. Fish. Aquat. Sci.* 41:521-525.

Fishelson, L. 1977. Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Elat (Gulf of Aqaba), Red Sea. *Isr. J. Zool.* 26:114-134.

Gotshall, D. W. 1977. Stomach contents of northern California Dungeness crabs, *Cancer magister*. *Calif. Fish Game* 63:43-51.

Hobson, E. 1968. Predatory behavior of some shore fishes in the Gulf of California. *U. S. Fish Wildl. Serv. Res. Rep.* 73: 92 p.

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

Malinowski, S. M. & R. B. Whitlatch. (In Press) Natural survivorship of young hard clams (*Mercenaria mercenaria*) in eastern Long Island Sound. *J. Shellfish Res.* 5(1): in press.

Möller, P. & R. Rosenberg. 1983. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in shallow marine waters, western Sweden. *Ophelia* 22:33-55.

Pratt, D. M. & D. A. Campbell. 1956. Environmental factors affecting growth in *Venus mercenaria*. *Limnol. Oceanogr.* 1:2-17.

Turner, H. J. 1948. Report on investigations of the propagation of the soft-shell clam, *Mya arenaria*. Woods Hole, MA: *Woods Hole Oceanogr. Inst. Contrib.* 462:61 p.

Virnstein, R. W. 1976. The effects of predation by epibenthic crabs and fishes on benthic infauna in Chesapeake Bay. Williamsburg, VA: Col. of William and Mary. Available from: University Microfilms, Ann Arbor, MI. Publication No. 76 - 17299. 86 p. Dissertation.

Journal of Shellfish Research, Vol. 4, No. 2, 145-153, 1984.

OBSERVATIONS ON THE FISHABLE POPULATION OF THE STONE CRAB *MENIPPE MERCENARIA* (SAY) IN SOUTH CAROLINA WATERS[1]

ELIZABETH L. WENNER AND ALVIN D. STOKES
Marine Resources Research Institute
South Carolina Wildlife and Marine Resources Department
P. O. Box 12559
Charleston, South Carolina 29412

ABSTRACT Collections of the stone crab *Menippe mercenaria* (Say) were made at 7 locations near Charleston, SC, from July to September 1982. In each location sampled, 5 wire, commercial blue crab (*Callinectes sapidus* Rathbun) traps with 2 entrance holes and 5 wooden-lath stone crab traps, similar to those used in the Florida fishery, were fished for 2 and 3 days in paired sets. Twice as many stone crabs were collected in the blue crab traps as in the stone crab trap, and for 6 of the sites sampled, catches in the blue crab trap were significantly greater than those in the stone crab trap. No significant differences were found in the number of stone crabs per trap between 2-day and 3-day sets for either trap type. The frequency distributions of carapace width (CW) for male, female, and ovigerous females of *M. mercenaria* indicated that traps were primarily sampling those stone crabs that were > 65 mm CW. The frequency distribution of propodus length (PL) showed that most of the males collected had at least one harvestable claw. Mean PL for male stone crabs ($\bar{x}$ = 85 mm) was greater than that for females ($\bar{x}$ = 69 mm). Incidence of missing claws was small, with 12% of the crabs missing one claw and 6% missing both claws. Sex ratios indicated dominance by females of *M. mercenaria*, with most ovigerous in July.

KEY WORDS: *Menippe mercenaria*, stone crab, fisheries, decapod Crustacea, South Carolina

INTRODUCTION

The stone crab *Menippe mercenaria* (Say) ranges from the Yucatan peninsula of Mexico, along the Gulf coast, into the Caribbean, and along the east coast of the United States to Cape Hatteras, North Carolina (Rathbun 1930, Williams 1965, Powers 1977). Stone crabs occur from the intertidal zone (McRae 1950) to 54 m depth (Bullis and Thompson 1965).

Despite its wide geographic range in warm temperate, subtropical, and tropical waters, the North American commercial utilization of *M. mercenaria* is confined primarily to Florida where its fishery constitutes the third largest crustacean fishery. At present, there is no directed fishery for *M. mercenaria* in South Carolina. Stone crab claws which are sold commercially are taken almost exclusively from individuals caught in crab pots being fished for blue crabs (*Callinectes sapidus* Rathbun). Although no data exist to document whether catches of *M. mercenaria* have increased in South Carolina in recent years, the demand for claws is greater. Stone crab claws have become a regular saleable item at many South Carolina seafood markets, and landing reports are now required for all seafood dealers.

This paper describes the results of a study to determine South Carolina's potential for expanded commercial utilization of *M. mercenaria*. Specific research objectives were to determine whether catches of stone crabs in South Carolina could be improved by adopting the trap used in the Florida fishery, whether duration of trap immersion affected catches, and to describe the size and sex composition of the catch.

MATERIALS AND METHODS

Field Sampling

Collections of stone crabs were made at seven locations near Charleston, SC, from July to September 1982 (Figure 1). Beatty's Creek, Whitesides Creek, and Capers Creek are located behind Capers Island off the Intracoastal Waterway. Whereas Whitesides Creek and Capers Creek are large and have numerous smaller creeks feeding into them, Beatty's Creek is narrow and dry, about 0.5 km from the mouth at low tide. The remaining locations (Lighthouse Creek, Lighthouse Inlet, Morris Island, and Breach Inlet), which are immediately adjacent to the Atlantic Ocean, have swifter water flow and steeper banks than the other sites. Exploratory fishing revealed that not every chosen site consistently yielded stone crabs; therefore, sampling at some locations was discontinued after one month if catches were low, and an alternate site was selected. Locations were sampled according to the following schedule: Beatty's Creek (July), Lighthouse Creek (July), Whitesides Creek (August), Capers Creek (August), Morris Island (August and September), Breach Inlet (September), and Lighthouse Inlet (July - September).

In each location five vinyl-coated wire, blue crab traps, each with two entrance holes, and five wooden-lath, stone

[1]This work is a result of research sponsored by the Gulf and South Atlantic Fisheries Development Foundation under Contract GASAFDI No. 21-07-9950 and by the South Carolina Wildlife and Marine Resources Department. Contribution No. 177 from the Marine Resources Research Institute.

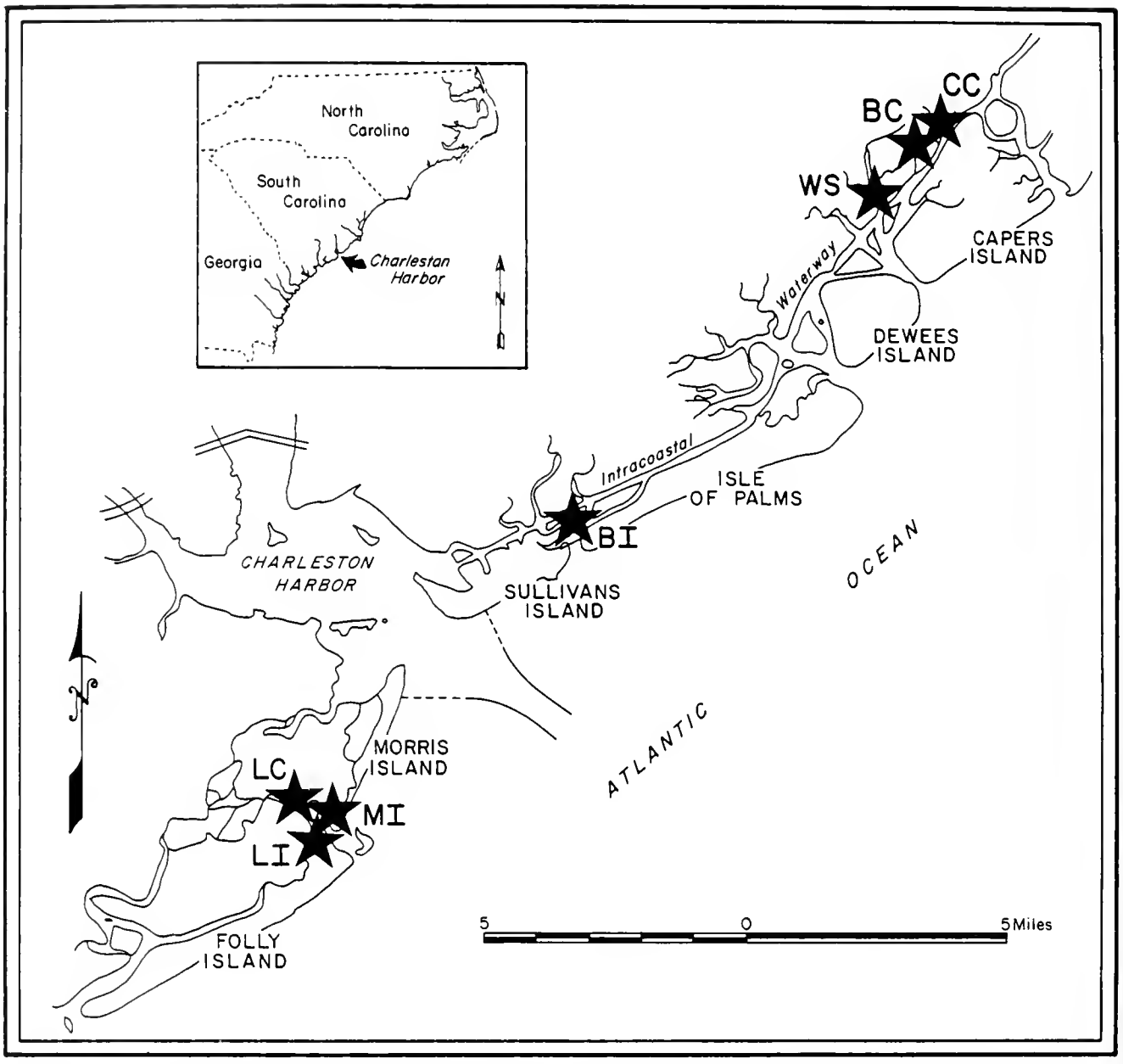


FIGURE 1. The seven sites where traps were deployed. LC = Lighthouse Creek, LI = Lighthouse Inlet, MI = Morris Island, BI = Breach Inlet, WS = Whitesides Creek, BC = Beatty's Creek, CC = Capers Creek.

crab traps, similar to those used in the Florida fishery, were fished for two or three days in paired sets. Occasionally, poor weather conditions prevented fishing of paired sets every two or three days. Stone crabs that were collected from longer trap sets were not included in analyses of relative abundance but were used in analyses of size and sex composition. A paired set consisted of a blue crab trap attached via a 9-m length of 6.35 mm diameter polypropylene line to a stone crab trap. The pair of traps was then attached by polypropylene line to a wooden stake driven into the creek bank. Although the length of line attaching each paired set to a stake varied with location, it was always long enough for the traps to remain submerged at normal low tides. During extremely low tides, the traps were at least partly submerged. Although traps were set perpendicular to the bank, strong tidal action, especially at the inlet sites, frequently moved traps closer to the bank and into shallower water. Staking of traps was preferred to using floats since this method minimized theft and poaching. Whereas stakes were not visible at maximum flood or high slack tide, all traps were fished and rebaited (with menhaden) at late ebb, low slack, or early flood tide. Surface temperature, salinity, and tidal stage were recorded during each site visit.

For each trap pulled during 2- and 3-day sets, the total catch of *M. mercenaria* and *C. sapidus* was recorded. Where possible, additional information were taken from every stone

TABLE 1.

Extremes (minimum and maximum) and mean ($\bar{x}$) temperature and salinity at sampling sites during July, August, and September 1982.

	JULY						AUGUST						SEPTEMBER					
	Temperature			Salinity			Temperature			Salinity			Temperature			Salinity		
	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max
Lighthouse Inlet	29	28	30	29	27	30	29	28	32	31	28	34	28	27	29	32	30	32
Lighthouse Creek	28	28	30	30	30	30	Not Sampled						Not Sampled					
Morris Island	Not Sampled						29	28	32	31	28	34	28	27	29	32	30	32
Breach Inlet	Not Sampled						Not Sampled						27	25	29	34	34	25
Beatty's Creek	30	26	36	32	30	34	Not Sampled						Not Sampled					
Capers Island	Not Sampled						29	28	31	33	30	35	Not Sampled					
Whitesides Creek	Not Sampled						29	28	31	34	32	36	Not Sampled					

TABLE 2.

Number of *M. mercenaria*, number of trap hauls, and catch per trap haul (C/T) for the stone crab trap and blue crab trap at each site. Summary of results of analysis of variance to determine significant differences in transformed [log (x + 1)] catch per trap haul between the two trap types is shown.

	STONE CRAB TRAP			BLUE CRAB TRAP			ANOVA RESULTS		
	No. Crabs	No. Trap Hauls	C/T	No. Crabs	No. Trap Hauls	C/T	F	df	P
Beatty's Creek	18	30	0.60	54	29	1.86	7.24	1/10	< 0.05
Lighthouse Creek	16	30	0.53	49	28	1.75	10.39	1/10	< 0.01
Whitesides Creek	13	30	0.43	47	30	1.57	19.35	1/10	< 0.01
Capers Creek	1	30	0.03	13	30	0.43	7.88	1/10	< 0.05
Morris Island	48	55	0.87	113	55	2.05	4.57	1/22	< 0.05
Breach Inlet	18	29	0.62	61	28	2.18	7.70	1/10	< 0.05
Lighthouse Inlet	134	86	1.56	196	81	2.42	3.32	1/35	> 0.05
TOTAL	248	290		533	281				

TABLE 3.

Number of *M. mercenaria*, number of trap hauls, and catch per trap haul (C/T) for the stone crab traps and the blue crab traps for each month of the study. Summary of results of analysis of variance to determine significant differences in transformed [log (x + 1)] catch per trap haul between the two trap types is shown.

	STONE CRAB TRAPS			BLUE CRAB TRAPS			ANOVA RESULTS		
	No. Crabs	No. Trap Hauls	C/T	No. Crabs	No. Trap Hauls	C/T	F	df	P
July	103	89	1.16	156	85	1.84	2.78	1/35	> 0.05
August	69	117	0.59	243	116	2.09	19.22	1/46	< 0.01
September	76	84	0.90	134	80	1.68	7.52	1/34	< 0.05

crab trapped including sex, carapace width (CW, measured as the maximum distance across the carapace between the posterior-most pair of lateral teeth), propodus length of the major cheliped or, where only one claw was present, the remaining cheliped (PL, measured as the distance along the lower margin from the tip of the fixed finger to the proximal end of the palm), weight, handedness (side with crusher), mission chelipeds, and stridulatory pattern (Savage et al. 1975). All collected stone crabs were tagged and released near the capture site. Tagging was not done for purposes of population assessment but merely to identify previously caught crabs so data would not be duplicated.

Data Analyses

Catch-per-unit-of-effort (CPUE), expressed as number of crabs per trap and number of crabs per trap per day, was used to evaluate abundance of *M. mercenaria*. After testing for homogeneity of variances, one-way analysis of variance was performed on catch data to determine whether differences in catch occurred between duration of immersion, month of sampling or trap type.

Morphometric relationships of male and nonovigerous females of *M. mercenaria* for propodus length regressed on total width were determined by analysis of covariance. Following analysis of covariance, a functional regression equation (Ricker 1973) was calculated for each morphometric relationship. Increased growth variations are associated with crabs having recently regenerated appendages; therefore, only crabs with unregenerated claws, as indicated by normal stridulatory patterns, and those with beaded-normal patterns (Savage et al. 1975) were used in regression analyses. Heterogeneous variances precluded use of standard methods to test equality of means, so an approximate t-test (Sokal and Rohlf 1969) was used to determine whether differences existed between males and nonovigerous females for propodus length. The nonparametric Kruskal-Wallis test (Siegel 1956) was used to determine whether differences in carapace width occurred between sexes, stations, and months.

Sex ratios and the frequency of handedness in *M. mercenaria* were examined by chi-square analysis. The significance level for all statistical testing was 0.05.

RESULTS

Distribution, Relative Abundance, and Catch Composition

Description of Study Sites: All locations sampled were characterized by having salinities >28 ‰: hard bottom with sessile invertebrate growth, especially the whip cord *Leptogorgia virgulata* (Lamarck) and the red beard sponge *Microciona prolifera* (Ellis and Solander); and dense beds of the American oyster, *Crassostrea virginica* (Gmelin), fringing the creek banks. Although current flow and water depth differed among sites, hydrographic conditions of temperature and salinity were similar (Table 1). In addition variation in recorded values of temperature or salinity at the sampling sites throughout the study was small.

Relative Abundance: A total of 847 stone crabs were collected during the 3-mo study; however, only 781 stone crabs were taken during 2- or 3-day sets and included in analyses of relative abundance. Twice as many stone crabs were collected in blue crab traps as in stone crab traps. The difference in catch, expressed as number of stone crabs per

TABLE 4.

Number of *M. mercenaria*, number of trap hauls, and catch per trap haul (C/T) for 2- and 3-day immersion durations. Summary of analysis of variance to determine significant differences in transformed [log (x + 1)] catch per trap haul between 2- and 3-day immersion durations is shown.

	TWO-DAY			THREE-DAY			ANOVA RESULTS		
	No. Crabs	No. Trap Hauls	C/T	No. Crabs	No. Trap Hauls	C/T	F	df	P
Stone crab trap									
July	55	44	1.25	48	45	1.07	0.02	1/17	>0.05
August	38	59	0.64	31	58	0.53	0.09	1/22	>0.05
September	49	43	1.14	27	41	0.66	3.30	1/16	>0.05
Blue crab trap									
July	65	43	1.51	91	42	2.17	1.16	1/16	>0.05
August	115	58	1.98	128	58	2.21	0.03	1/22	>0.05
September	77	41	1.88	57	39	1.46	0.69	1/16	>0.05

TABLE 5.

Number of individuals measured (n), extremes, mean ($\bar{x}$), and standard error ($s_{\bar{x}}$) of carapace width and propodus length for male, female, and ovigerous stone crabs.

	CARAPACE WIDTH (mm)				PROPODUS LENGTH (mm)			
Sex	n	Extremes	$\bar{x}$	$s_{\bar{x}}$	n	Extremes	$\bar{x}$	$s_{\bar{x}}$
Male	242	13-129	95	0.93	175	36-126	85	1.34
Female	425	50-120	92	0.53	328	39-98	69	0.54
Ovigerous Female	160	65-112	88	0.76				

trap, was found to be statistically significant ($t = -3.60$, 12 df, $P < 0.05$) between the two trap types. Furthermore, the transformed ($\log_{10}[x+1]$) number of *M. mercenaria* per trap was significantly greater for the blue crab trap at every site except Lighthouse Inlet (Table 2) and during each month of the study except July (Table 3). A one-way analysis of variance revealed no significant difference in transformed ($\log_{10}[x + 1]$) number of *M. mercenaria* per trap per day between months for either the stone ($F = 2.85$, 2/58 df, $P > 0.05$) or blue crab trap ($F = 0.07$, 2/51 df, $P > 0.05$).

No consistent differences in catch-per-unit-of-effort were noted between immersions of 2- and 3-days for either trap type (Table 4). Analysis of variance confirmed that no significant difference in the transformed ($\log_{10}[x + 1]$) number of stone crabs per trap existed between 2- and 3-day immersions for either the stone or blue crab traps (Table 4).

Size and Sex Composition

Frequency distributions for CW (grouped into 5-mm size classes) of the 827 stone crabs measured indicated that traps were primarily sampling those stone crabs that were > 65 mm. The frequency distribution for sampled male crabs was bimodal with peaks at 95 and 105 mm, whereas the distributions of nonovigerous and ovigerous females were unimodal with peaks at 95 and 90 mm, respectively. Mean CW of male crabs was greater than that for females or ovigerous females (Table 5). Ovigerous females had the smallest mean CW of the trappable population. The Kruskal-Wallis test indicated that significant differences in median CW existed between males, females, and ovigerous females ($H = 17.367$, df = 2, $P < 0.01$).

The frequency distribution of PL grouped into 5-mm size classes for male and nonovigerous females of *M. mercenaria* having normal or beaded-normal stridulatory patterns showed that most (82%) of the males collected had at least one legally harvestable claw. South Carolina law stipulates that only the larger of the two claws of a stone crab may be removed and that the removed claw must have a propodus length of at least 70 mm. Modal PL for males occurred at 80 and 100 mm. In contrast, modal PL for females was 65 mm, with slightly over half (51%) of the females measured having a legal-sized claw of ≥ 70 mm PL. For the total sample of crabs (n = 503) for which the PL was measured, 54% possessed at least one claw of legally harvestable size. An approximate t-test indicated that the mean PL for male crabs ($\bar{x} = 85$ mm) was significantly greater than that for females ($\bar{x} = 69$ mm) ($t'_S = 11.39$, $P < 0.05$).

Examination of mean carapace width and propodus length by sampling site reflected stable areal distribution by size of *M. mercenaria* in the study area. Differences between means were not assessed because of drastically unequal sample sizes. For each site sampled, the mean PL was greater than 70 mm, the size of a legally harvestable claw. Frequency distributions of CW and associated statistics were also examined by month. The Kruskal-Wallis test indicated that median CW of all crabs sampled was significantly different between months ($H = 11.853$, df = 2, $P < 0.01$); however, inspection of means revealed a relatively stable temporal distribution of *M. mercenaria* by size: July ($\bar{x} = 90.1$ $s_{\bar{x}} = 0.080$, n = 253), August ($\bar{x} = 93.4$ $s_{\bar{x}} = 0.59$, n = 356), September ($x = 92.2$, $s_{\bar{x}} = 0.83$, n = 218).

Analysis of covariance between carapace width (x) and propodus length (y) for males and nonovigerous females revealed significant differences in slope, elevation, and

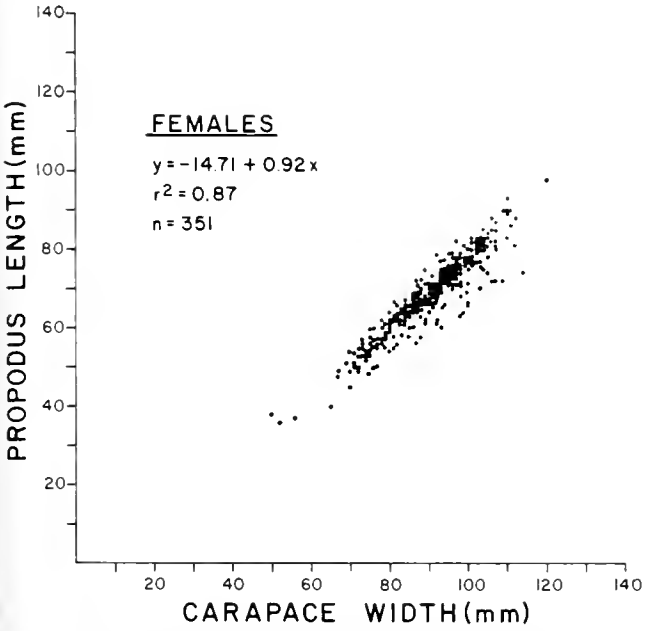


Figure 2. Relationship between propodus length of major cheliped and carapace width of female stone crabs.

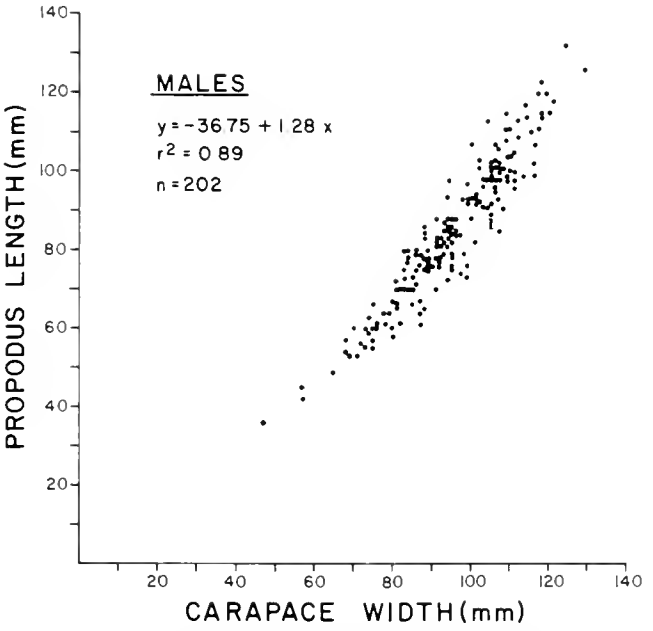


Figure 3. Relationship between propodus length of major cheliped and carapace width of male stone crabs.

variance (F_{reg} = 118.9, 1/549 df; $F_{adj.\ mean}$ = 654.2, 1/550 df; F_{var} = 2.7, 200/349 df). Thus, separate functional regression equations for males and females were calculated to explain the relationship between CW and PL (Figure 2 and 3). Regression analysis revealed that males entering our traps had harvestable claws at CW $\geq$ 83 mm, whereas harvestable claws of females occurred at CW $\geq$ 92 mm.

The incidence of missing claws among the 842 stone crabs collected in the study was small. Only 12% of the individuals were missing one claw, while 6% were missing both claws. Among individuals having both claws, right major claws occurred more than twice as frequently as left major claws, indicating that left-handed crabs constituted only about 38% of the population. The deviations from 1:1 ratio were significant for males (χ^2 = 37.07, $P < 0.01$), females (χ^2 = 61.6, $P < 0.05$), and ovigerous females (χ^2 = 16.0, $P < 0.05$).

Examination of stridulatory patterns of the major cheliped for 769 sexed crabs possessing both claws and the remaining cheliped for crabs having one claw revealed that > 70% of males, females, and ovigerous females had claws with the normal pattern, indicating an unregenerated claw. Claws with other stridulatory patterns (dotted, dashed, and beaded-normal) representing successive stages in regeneration of the claw (Savage et al. 1975) constituted 22, 23, and 27% of the males (n = 220), females (n = 390), and ovigerous females (n = 159) sampled, respectively.

Monthly sex ratios indicated significant dominance by females, which constituted 73% of the sexed crabs in July, 69% in August, and 71% in September (Table 6). Most females caught in July were ovigerous (48%), with a marked reduction occurring in September. Examination of the egg masses revealed that 68% of the ovigerous females in July carried orange eggs, indicative of recent spawning. The proportion of ovigerous females bearing orange eggs increased to 77% in August.

DISCUSSION

Reported landings in South Carolina of stone crab claws which totaled 1,790 kg (3,943 lb) in 1982, and the results of trapping studies, suggest that stocks of *M. mercenaria* are not sufficient to support an intensive, directed fishery. Although landings of stone crab claws in South Carolina may increase because of added interest and awareness of the potential for a fishery, it is unlikely that the population of *M. mercenaria* could withstand the level of fishing effort found in the Florida fishery without adverse effects. Estimates of effort in Florida for 1979-1980 showed that 297,600 traps were deployed from 291 boats, resulting in a reported commercial catch ($\sim 8.63 \times 10^5$ kg; $\sim 1.9 \times 10^6$ lb) of stone crab claws valued at $5,135,472 (Zuboy and Snell 1980). Based on results of our study, it is hypothesized that CPUE would not be as high as 2.72 kg (6 lb) claws/trap which is the 1980 CPUE for the Florida fishery (Zuboy and Snell 1980); however, until data are available on effort and yield of claws from commerical crabbing operations in South Carolina, it will be impossible to properly assess existing stocks of *M. mercenaria*.

Although all areas fished during our study were characterized by high salinities and live oyster beds, CPUE of *M. mercenaria* was highly variable between locations. The creek sites, which had less steep banks and slower currents than the inlets, yielded fewer stone crabs. Catches per month were highest for the Lighthouse Inlet and Morris Island sites, which were immediately adjacent to the ocean. Possible explanations for the differences in catches among areas include differences in suitability of substrate for burrowing and availability of shelter for protection from predators. Published information on the distribution of *M. mercenaria* indicates that adults dwell on a variety of bottom types, including grassflats (McRae 1950), rocky or shell bottom (McRae 1950, Whitten et al. 1950, Powell and Gunter 1968), and sand and mud (Powell and Gunter 1968). In southwestern Florida, adult stone crabs characteristically inhabit burrows on turtle grass (*Thalassia testudinum* Konig) flats or along the banks of channels (Bender 1971). Bender (1971) found that CPUE changed with season and sediment type. Seagrass flats consistently yielded more crabs than did mud bottom where crabs had difficulty digging and maintaining open burrows (McRae 1950). In Texas and northwestern Florida, stone crabs inhabit oyster reefs (Powell and Gunter 1968) and rock jetties (Whitten et al. 1950). Apparently, the shell substrate of oyster reefs provides reinforcement for creation of stable burrows, as well as protection from predators.

Comparisons between catches of *M. mercenaria* (no./trap) in stone crab and the wire blue crab traps clearly indicated superiority of the latter. Stone crabs are primarily caught incidentally to blue crabs making it unnecessary to adopt new gear in order to maximize stone crab catches in South Carolina. Nevertheless, the unquestionable success of the wooden trap in the Florida fishery begs an answer to the question of why its catches were significantly lower in South Carolina. The preliminary nature of this study permits only speculation about differences in trap performance. The design of a trap affects the crab's success of entry and the trap's maximum catch (Miller 1980); thus, the difference in entrance design between the traps is one possible explanation. Location of the entrance has been shown to affect trap

TABLE 6.

Numbers of male and female stone crabs, and the percent of female crabs bearing eggs for each month of study. Sex ratios (F:M) significant at $\alpha = 0.05$ are marked with asterisks.

	July	August	September
Male	68	110	64
Female	185	246	154
% ovigerous	43	29	6
Ratio F:M	2.7:1*	2.2:1*	2.4:1*

catches (Miller 1980). In the blue crab trap, two opposite funnel-shaped entrances which sloped upward from the bottom of the trap permitted entrance by crabs, whereas the smaller stone crab trap provided a single top entrance which, according to Florida statutes, must be no larger than 10.2 x 16.5 cm (Bert et al. 1978).

Miller (1979) found that the most effective trap design is one in which the bait odor leads crabs to the trap entrance, not to the trap. He found that the red crab *Cancer productus* (Randall) entered the side entry trap more frequently than the top entry trap, if opposing entrances were parallel to the current. Furthermore, Miller (1979) found that a greater percentage of *C. productus* entered the side entry trap in the first hour of observation; and that because of their success in finding an entrance, there were few agonistic encounters resulting from an accumulation of *C. productus* around the base of the trap. By closing the two side entrances of lobster traps and fitting a top entrance, Stasko (1975) found that catches of the American lobster *Homarus americanus* H. Milne Edwards decreased. Similarly, Kessler (1969) obtained greater catches of spot prawn *Pandalus platyceros* Brandt in traps with a long-tunnelled side entrance, and lower catches in traps with a top entrance. The poorer performance of the top entrance traps may result from the crustaceans circling the base of the traps rather than swimming or crawling over them.

A similar comparison between trap types needs to be done in southwestern Florida, where the habitat of *M. mercenaria* is markedly different from that in South Carolina. The clarity of water in the Florida Bay area may be a factor which favors use of the wooden trap since stone crabs may readily enter the trap which provides the most shelter. This may not be the case in South Carolina where estuarine waters are turbid.

The lack of a significant difference in catches between immersion durations for the two trap types that were tested reflects the findings of Miller (1980) that trap catches of decapod crustaceans routinely do not increase in proportion to immersion duration. In fact, studies have shown that the mean catches do not usually approach the maximum capacity of the traps, but are limited by saturation of the trap (Robinson and Dimitrion 1963, Sinoda and Koyayasi 1969, Krouse and Thomas 1975, Skud 1979). Miller (1980) found that trap saturation can start limiting catches of the rock crab *Cancer irroratus* Say and the toad crab *Hyas araneus* (Linnaeus) after 4-6 h. Catches do not increase beyond this time because additional entrants to traps are countered by those that escaped. He attributed trap saturation to threat displays and intimidation by *C. irroratus* and *H. araneus* inside traps which discouraged those outside from entering. In the Florida fishery for *M. mercenaria*, it is not unusual for traps to be immersed 10 to 15 days prior to being pulled (R. Bruland, Keys Fisheries, Marathon, FL, pers. comm., 1982). With lengthy immersion, it is expected that the total catch per trap haul would peak and perhaps even decrease because of either escape from or mortality in the trap (Austin 1977).

Carapace width frequencies of *M. mercenaria* from Florida suggest that South Carolina stone crabs may become trappable at a CW of > 45 mm (Sullivan 1979). In Florida, stone crabs that range from 45 to 60 mm CW represent the first year class (one + years old). In the trappable portion of the Florida population, the two large size classes for each sex overlap, with sizes for males centered around 80-103 mm CW and a major mode for females found at 80-100 mm CW. Size comparisons between the sexes showed that the mean CW for males was larger than for female crabs in Florida (Bender 1971) as well as South Carolina. Bender (1971) attributed sexual differences in size to molting of males when females were spawning. Stone crabs of both sexes from Florida that measured $\sim$ 80 mm CW were about 2 years-old, whereas those around 100 mm CW were primarily Year-III crabs with some contribution by Year-IV individuals (Sullivan 1979). In the Florida population, smaller crabs (45-60 mm CW) were observed in summer when waters are closed for trapping. Modal sizes for both sexes were greatest in winter and spring and tend to remain high through summer. Sullivan (1979) indicated that modal size for females declined in October and November, whereas this decline occurred during September and October for male stone crabs. Bender (1971) found that most *M. mercenaria* measured < 60 mm CW and > 95 mm CW in late fall. He attributed this to recruitment from juvenile stone crabs which reached sexual maturity in fall. Year-round information is clearly needed on *M. mercenaria* from South Carolina before any assessment of recruitment or year-class strength can be obtained and relevant comparisons made with Florida stocks.

The carapace width at which stone crabs of both sexes from South Carolina possess legally harvestable claws (≥ 70 mm) is comparable to that in the Florida population. Our results showed that male stone crabs attained harvestable claws at ≥ 83 mm CW whereas females possessed legal-sized claws at ≥ 92 mm CW. In Florida, where a legal-sized claw is also ≥ 70 mm, males and females attained harvestable major claws at about 80 and 87 mm CW, respectively (Sullivan 1979). Furthermore, male claws for all carapace widths were larger than those for equal-sized females in collections from South Carolina and Florida. The smaller size of claws from females is probably related to differential growth rates of male and female crabs. Sullivan (1979) noted that female stone crabs exhibited smaller mean incremental carapace width and claw growth increases than did male crabs.

Slightly over one-half of the stone crabs sampled during this trapping study possessed at least one legally harvestable claw. A high incidence of the normal stridulatory pattern indicated that most of the stone crabs sampled had not regenerated a claw. Normal claws also account for a high percentage of claws in the Florida fishery (Savage et al. 1975). Savage et al. (1975) hypothesized that incidence of regenerated claws is influenced by water temperature. Consequently, the largest frequency of regenerated claws from Florida stone crabs occurred in the first months of the

legal fishing season, which begins in October, because water temperature during the preceding summer was conducive to rapid growth and claw regeneration.

Right-handed stone crabs predominated in Florida as well as South Carolina. Savage et al. (1975) found that right-handed crushers were nearly three times as common as left-handed crushers in Florida. Cheung (1976) implied that right-handedness was normal for *M. mercenaria*. He hypothesized that left-handedness was developed secondarily through claw reversal after the autotomy of the crusher found on the right. This hypothesis is supported by Savage et al. (1975) as well as the present study with observations of claws that were intermediate between crushers and pincers.

The predominance of females in samples taken during the summer was reported by McRae (1950), Noe (1967), and Bender (1971) for the Florida population. They indicated that sexual dominance changes seasonally, such that trapped males predominate in winter. Several explanations have been proposed concerning seasonal changes in sexual dominance. Sullivan (1979) suggested that decreases in relative numbers of legal-sized males over the duration of the fishing season (Oct - May) resulted from harvest-induced mortality. In addition, seasonal onshore or offshore movements by the different sexes may affect sex ratios observed in a particular area. Bender (1971) also noted that seasonal differences in sex ratios indicate a seasonal migration, primarily by one sex. Bert et al. (1978) surmised that this directional movement was primarily by males that move shoreward to mate with molting females that were year-round residents of shallow grassflats. Other non-directional movements (*sensu* Bert et al. 1978) have also been reported for the Florida population and may be attributed to increased activity of stone crabs following storms and strong northeasterly winds (R. Bruland, Keys Fisheries, Marathon, FL, pers. comm.). Whether similar seasonal changes in sex ratios occur in the South Carolina population remains to be determined.

The spawning season, determined by the presence of ovigerous female stone crabs was reported by Williams (1965) to extend from May through July in North Carolina. Bert et al. (1978) noted that the spawning season lengthens in duration toward the southern part of the geographic range of *M. mercenaria*, so that ovigerous female crabs were found throughout the year in southwestern Florida. Temperature was the most important factor influencing reproduction, with optimum ovarian development occurring at 28°C (Cheung 1969). If a strong spawner-recruit relationship is present for *M. mercenaria*, the apparently limited spawning season in South Carolina may be one explanation for lower relative abundance of stone crabs than in Florida.

ACKNOWLEDGMENTS

It would have been impossible to carry out this project without the generous help of personnel from the SC Wildlife and Marine Resources Dept., interested friends, and commercial crabbers. Thanks are extended to everyone who participated in the field sampling, and especially to L. Burgess, C. Wenner, R. Beatty, J. Williams, S. Newsom, W. Jenkins, and R. Smiley who volunteered on a regular basis. We are most grateful to D. Cupka and G. Ulrich who supplied designs of the Florida trap. Glenn Ulrich, along with R. Low, D. Oakley, N. Jenkins, W. McCord, and W. Seaborn, helped to construct the Florida traps. Ben Moise (Law Enforcement Division) and J. Bishop (MRRI) kindly supplied most of the blue crab traps. Ray Rhodes (SCWMRD), P. Eldridge (NOAA), and T. Bert (Yale University) supplied some literature and information on the Florida fishery. Dale Theiling and J. Smith (SCWMRD) made available their information on 1982-83 stone crab landings from South Carolina. Technical assistance was provided by K. Swanson who drafted the figures; G. Gash, L. Rigsbee, and J. Stribling who assisted with data processing; and N. Beaumont who typed the manuscript. Comments by G. Sedberry, D. Whitaker, and an anonymous reviewer improved the manuscript.

REFERENCES CITED

Austin, C. B. 1977. Incorporating soak time into measurement of fishing effort in trap fisheries. *U.S. Fish. Wildl. Serv. Fish. Bull.* 75:213-218.

Bender, E. S. 1971. Studies of the life history of the stone crab *Menippe mercenaria* (Say), in the Cedar Key Area. Gainesville, FL: Univ. of Florida. 110 p. thesis.

Bert, T. M., R. E. Warner & L. D. Kessler. 1978. The biology and Florida fishery of the stone crab *Menippe mercenaria* (Say), with emphasis on southwest Florida. Gainesville, FL: State Univ. System of Florida, Sea Grant College Program. Tech. Pap. 9:82 p.

Bullis, H. R., Jr. & J. R. Thompson. 1965. Collections by the exploratory fishing vessels *Oregon, Silver Bay, Combat,* and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. *U.S. Fish. Wildl. Serv. Spec. Sci. Rep.* 150:130 p.

Cheung, T. S. 1969. Endocrine control of growth and reproduction in the stone crab *Menippe mercenaria* (Say). *Am. Zool.* 7(2):200 (Abstract).

———. 1976. A biostatistical study of the functional consistency in the reversed claws of adult male stone crabs *Menippe mercenaria* (Say). *Crustaceana* 3:137-144.

Kessler, D. W. 1969. Test tank studies in shrimp-pot efficiency. *Fish. Ind. Res.* (U.S. Natl. Mar. Fish. Serv.) 5:151-160.

Krouse, J.S. & J. C. Thomas. 1975. Effects of trap selectivity and some population parameters on size composition of the American lobster *Homarus americanus* catch along the Maine coast. *U.S. Fish. Wildl. Serv. Fish. Bull.* 73:862-871.

McRae, E. D., Jr. 1950. An ecological study of the xanthid crabs in the Cedar Key area. Gainesville, FL: Univ. of Florida. 72 p. Thesis.

Miller, R. J. 1979. Entry of *Cancer productus* to baited traps. *J. Cons. Cons. Int. Explor. Mer.* 38:220-225.

_____. 1980. Design criteria for crab traps. *J. Cons. Cons. Int. Explor. Mer.* 39(2):140-147.

Noe, D. C. 1967. Contribution to the life history of the stone crab *Menippe mercenaria* (Say) with emphasis on the reproductive cycle. Miami, FL: Univ. of Miami. 55 p. Thesis.

Powell, E. H., Jr. & G. Gunter. 1968. Observations of the stone crab *Menippe mercenaria* (Say) in the vicinity of Port Aransas, Texas. *Gulf. Res. Rep.* 2(3):285-299.

Powers, L. W. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. *Contrib. Mar. Sci. Suppl.* 20:190 p.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. *U.S. Natl. Mus. Bull.* 152:609 p.

Ricker, W. E. 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.* 30:409-434.

Robinson, R.K. & D. E. Dimitrion. 1963. The status of the Florida spiny lobster fishery, 1962-63. *Fla. Board Conserv. Tech. Ser. (Fla. Mar. Res. Publ. Tech. Ser.)* 42:30 p.

Savage, T., J. R. Sullivan & C. E. Kalman. 1975. An analysis of stone crab (*Menippe mercenaria*) landings on Florida's west coast, with a brief synopsis of the fishery. *Fla. Mar. Res. Publ.* 13:37 p.

Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences.* New York, NY: McGraw-Hill. 312 p.

Sinoda, M. & T. Kobayasi. 1969. Studies on the fishery of Zuwai crab in the Japan Sea - VI. Efficiency of toyama kayo (a kind of crab trap) in capturing benizuwai crab. *Bull. Jpn. Soc. Sci. Fish.* 35:948-956.

Skud, B. E. 1979. Soak time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* 175:190-196.

Sokal, R. R. & F. J. Rohlf. 1969. *Biometry.* San Francisco, CA: W. H. Freeman and Co. 776 p.

Stasko, A. B. 1975. Modified lobster traps for catching crabs and keeping lobsters out. *J. Fish. Res. Board Can.* 32:2515-2520.

Sullivan, J. R. 1979. The stone crab *Menippe mercenaria* in the southwest Florida fishery. *Fla. Mar. Res. Publ.* 36:37 p.

Whitten, H. L. , H. F. Rosen & J. W. Hedgepeth. 1950. The invertebrate fauna of Texas coast jetties; a preliminary survey. *Publ. Inst. Mar. Sci.* Univ. Tex. (*Contrib. Mar. Sci.*) 1:53-87.

Williams, A. B. 1965. The decapod crustaceans of the Carolinas. *U.S. Fish. Wildl. Serv. Fish. Bull.* 65(1)1-298.

Zuboy, J. R. & J. E. Snell. 1980. Assessment of the Florida stone crab fishery. NOAA Tech. Memo., NMFS-SEFC-21. 29 p. *U.S. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Southeast. Fish. Cen. Tech. Memo.* 21:29 p.

Journal of Shellfish Research, Vol. 4, No. 2, 155-159, 1984.

RESEARCH NOTE

RELATIVE GROWTH RATE CYCLES IN *CRASSOSTREA VIRGINICA* (GMELIN) FED FIVE ALGAL DIETS

RAVENNA UKELES, GARY H. WIKFORS AND JOSEPH W. TWAROG, JR.
National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460

ABSTRACT Juvenile oysters, *Crassostrea virginica* (Gmelin), were reared for 12 weeks in the laboratory within a chamber which provided a continuous flow of filtered, ultraviolet irradiated seawater (except during feeding). Each of the following species was utilized as a food source in these experiments: *Tetraselmis maculata* Butcher, *Thalassiosira pseudonana* Hasle and Heimdal, *Dunaliella euchlora* Lerche, *Phaeodactylum tricornutum* Bohlin, and a mixture of the latter two species. Changes in live weight and shell height were calculated in terms of relative growth rate. Analysis of variance demonstrated that *T. maculata* or *T. pseudonana* stimulated significantly greater increases in live weight of oysters than other diets of single algal species. Two peaks in live-weight relative growth rate separated by an interval of about 5 weeks were observed in each of the experimental feeding regimes. The cycle of relative growth rate in oyster weight was not apparent in shell height measurements. These data demonstrate that *C. virginica* is capable of producing a cyclic pattern of relative growth rate.

KEY WORDS: Cycles, algal diets, *Crassostrea virginica*

INTRODUCTION

Periodicity in valve movements of bivalve mollusks has been a subject of intense interest, and efforts have been made to correlate activity (valves open) with the diurnal and tidal cycles of the natural environment. The literature contains many differences of opinion as to whether there is a causal relationship only between exogenous rhythms of the environment and feeding in mollusks or if endogenous rhythms are also present (see Higgins [1980] for references). In this latter study on the feeding behavior of juveniles of *Crassostrea virginica* (Gmelin), activity was shown to be quantitatively regulated by the presence of algal foods; when food was present *C. virginica* was active a greater proportion of the time than when it was absent (Higgins 1980). Digestive rhythms in *Ostrea edulis* Linné were investigated in the laboratory by Langton and Gabbott (1974), who concluded that extracellular digestion in *O. edulis* is not endogenous but is controlled by feeding activity. Support for this contention was reported for two sublittoral populations of *O. edulis* observed *in situ* (Wilson and La Touche 1978). Studies with *Mytilus edulis* Linné collected from mid-tide level showed a correlation between amylase activity in the digestive gland and tidal heights, giving evidence of an imposed tidal rhythm in intracellular digestion (Langton 1977). Coordinated rhythms of digestion, absorption, and excretion of *M. edulis* that had seasonally dependent periodicities have been observed (Hawkins et al. 1983). A sublittoral bivalve, the scallop *Pecten maximus* Linné, was shown to orient itself to tidal currents and to demonstrate a 24-hour digestion cycle with feeding at each 12-hour tidal cycle (Mathers 1976). In contrast to the extensive literature on feeding and digestion rhythms in mollusks, the subject of periodicity in growth has received no attention with the exception of the study of growth patterns on the external surfaces of molluscan shells (Jones 1983).

To study the nutritional values of cultured microalgal species to juveniles of *C. virginica*, we utilized axenic algal cultures and molluscan rearing chambers (Ukeles and Wikfors 1982) designed to eliminate many of the variables that could obscure the oyster response to a particular algal food source. Upon inspection of oyster growth data thus obtained during two different years, a slight, but consistent variation in absolute growth curves became evident. Calculation of relative growth rates from live-weight determinations revealed the cyclic pattern in growth of juvenile oysters that is reported in this paper.

MATERIALS AND METHODS

Juvenile oysters used in this study were laboratory-reared and had initial live weights of 0.29-0.38 g/oyster. Experiments were conducted in the molluscan rearing chambers described in detail in Ukeles and Wikfors (1982). Oysters of similar initial size (as determined by visual observation) were cleaned, sorted into groups of 50 (except in one experiment where groups of 100 and 200 oysters were used), and placed on the Nitex®[1] monofilament nylon-mesh screen (Tetco, Elmsford, NY) of each chamber.

Seawater temperature was maintained at 26°C with immersion heaters controlled by thermoregulators. Seawater was filtered by passing it through a series of polypropylene filter cartridges: four filters connected in parallel with mean retentions of 50 μm, three filters in parallel with mean retentions of 10 μm, and one filter with a mean retention of 1 μm (Industrial Filters, Burlington, MA).

The algal foods utilized in experiments were axenic cultures of the following species: *Tetraselmis maculata* Butcher, *Thalassiosira pseudonana* Hasle and Heimdal,

[1]Use of trade names does not imply endorsement by the National Marine Fisheries Service.

Dunaliella euchlora Lerche, and *Phaeodactylum tricornutum* Bohlin. Algal cultures were produced in a semi-continuous culture system (Ukeles 1973) and harvested daily. The ration of algal food was added to each chamber in a single batch at the same time each day of the week, and oysters were permitted to feed on algal suspensions for four hours during which seawater flow was discontinued. The volumes of algal cultures introduced into the chambers were 0.6 ml packed cells as determined by centrifugation in modified Hopkins tubes (Ukeles 1973). Also, dry weights of algal cells were determined for each species according to the method of Epifanio and Ewart (1977). Oysters were fed 0.32-0.37 g dry weight of algae per 50 oysters each 24 hours, with the exception of *P. tricornutum* for which the dry weight was 0.22 g. These rations had been shown to be appropriate for nutritional support and did not result in the production of pseudofeces by oysters (Ukeles and Wikfors 1982).

Chambers were dismantled each week and scrubbed clean; seawater filters were replaced by new ones. At this time, oysters were rinsed to remove debris or food adhering to the surface of the shell, and dried on tissue paper to remove exterior moisture. Thus, live-weight determinations included shell weight, tissue weight, and tissue moisture. The weight per oyster was determined by taking the mean value of the mass of pooled groups of 50 oysters collected from each chamber. This method of determining weekly increments of oyster growth is practical for dealing with large numbers of small animals, has the advantage of including both shell and tissue weight (other methods are based upon shell deposition only [Andrews 1963]), and does not require the sacrifice of oysters. Thereby, growth curves could be plotted utilizing data collected from the same population each week. Wilbur and Owen (1964) noted that there are two methods of measuring growth. Absolute growth is a cumulative increase in mass (or length) with time represented as dm/dt, where m is mass and t is time. Relative growth is the growth increment per mass per unit time or dm/mdt. The relative growth rate would be the change in slope of the curve of dlog m/dt which on differentiation becomes dm/mdt (the expression given above). Our computation followed the formula given by Wilbur and Owen (1964) for instantaneous relative growth rate $K = \frac{dM/dt}{M}$ or $K = \frac{\ln/Mn/Mo}{t}$ where M_n and M_o are mean live weights at two times and t = 1 week. This formula is also expressed by Fisher (1938) as: $\frac{d}{dt}(\log_e m)$ where t = 1 week and m = mean live weight of oysters. With this calculation, the true mean value for the relative growth rate for one week is obtained from the natural logarithms of the successive weights. Relative rates of increase are multiplied by 100 and expressed as a percentage rate of increase per week.

To compare results obtained from live-weight determinations with linear measurements of shell height, photographs of the same population of oysters were taken every 14 days. Mean shell heights, determined by measuring projected photographic images, including a mm scale, were used to calculate relative growth rates of shell heights according to the previously cited formula.

RESULTS

The calculation of live-weight relative growth rate during 12 weeks of observation revealed a pattern of two peaks separated by 5- to 7-week intervals. This type of cycle was consistent for all experimental treatments although there were small variations in the time intervals between peaks.

Tetraselmis maculata, a species that supports excellent growth of juvenile oysters (Ukeles and Wikfors 1982), was fed to different populations of oysters in experiments conducted during July-September of 1980 and August-October of 1982. There was a strikingly similar pattern of live-weight relative growth rate in both experiments, although the overall growth was different for the two oyster populations (Figure 1). At an initial mean live weight of 0.382 g/oyster, the increase in 12 weeks was 140.8%, whereas at a smaller initial mean weight of 0.150 g/oyster, the increase in weight was 271.3%.

The observation that relative growth in general decreases with increasing size is consistent with the principles stated by Fisher (1938) and previous observations of shell growth in a number of molluscan species (Wilbur and Owen 1964). These phenomena were not apparent if live-weight

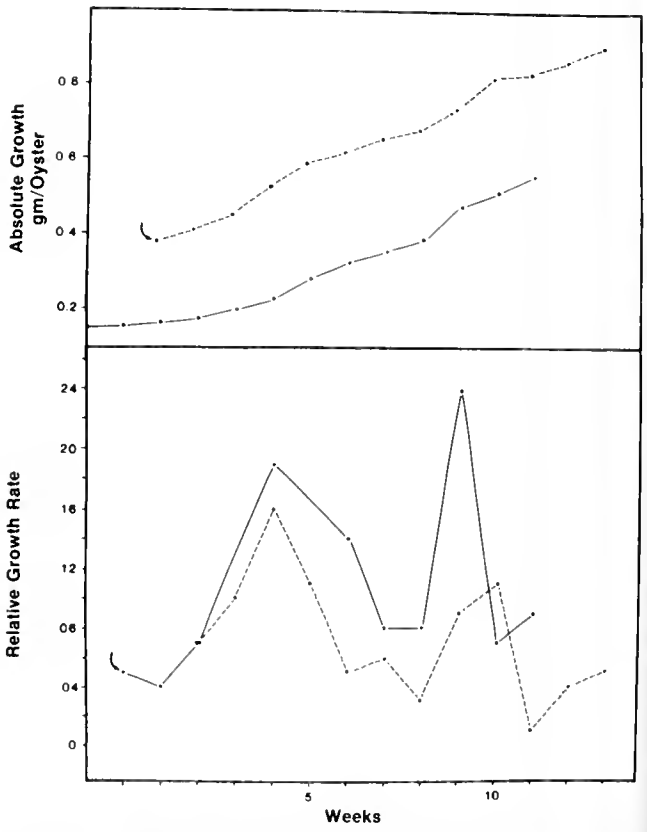


Figure 1. Absolute and relative growth of juvenile oysters (expressed in g live-weight) fed a diet of *Tetraselmis maculata* in experiments conducted in 1982 (• ——— •), and in 1980 (• ---------- •).

data were evaluated as absolute growth (Figure 1). Feeding oysters the diatom *T. pseudonana*, which also promotes rapid growth of juveniles of *C. virginica* (Epifanio et al. 1976, Ukeles and Wikfors 1982), yielded a cycle similar to that observed for *T. maculata*. Algal species that were of lesser nutritional value, *D. euchlora* and *P. tricornutum*, similarly resulted in two peaks in live-weight relative growth rate separated by an interval of 5 weeks (Figure 2). Analysis of variance indicated that relative growth of oysters fed *T. maculata* or *T. pseudonana* was significantly greater (α = 0.01) than oysters fed *D. euchlora* or *P. tricornutum* in experiments conducted in 1980. Growth of unfed oysters in the first several weeks of the experiment could be attributed to stored metabolic products accumulated prior to initiation of the experiment.

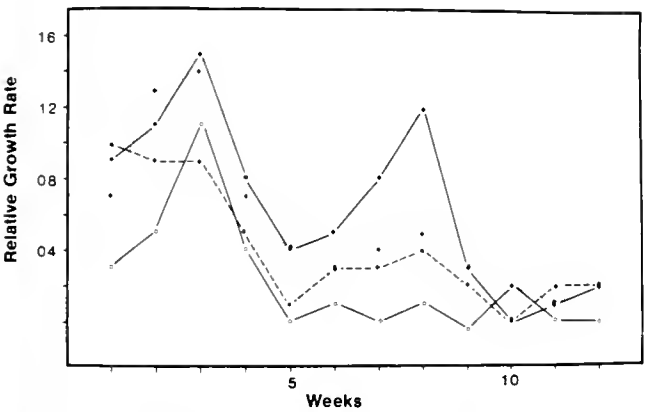


Figure 2. Live-weight relative growth of oysters fed diets of the following algal species: *Thalassiosira pseudonana* (• ——— •), *Dunaliella euchlora* (• ——— •), *Phaeodactylum tricornutum* (• ---------- •), and control (unfed) oysters (o ——— o).

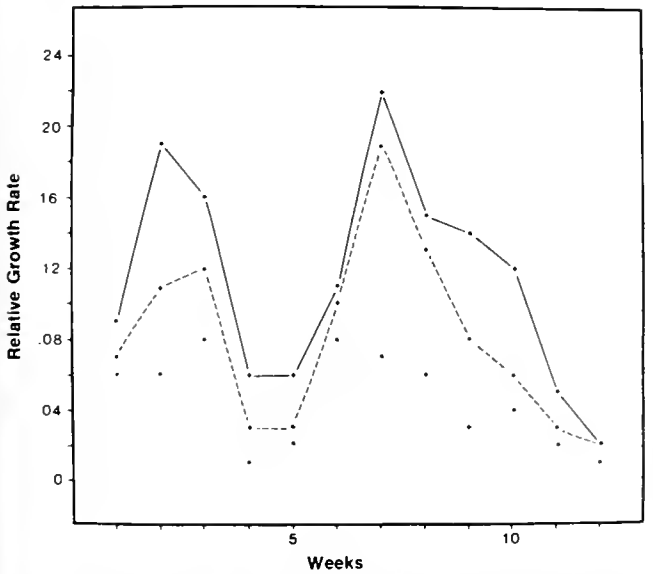


Figure 3. Live-weight relative growth of oysters fed equal suspensions of a mixture of *Phaeodactylum tricornutum* and *Dunaliella euchlora:* chambers containing 50 oysters (• ——— •), 100 oysters (• ----------•), and 200 oysters (• ---------- •).

It is well-documented that a diet consisting of a mixture of algal species is beneficial to the growth of larval and juvenile oysters (Davis and Guillard 1958, Epifanio 1979). We made a similar observation during June-August 1980 with oysters fed a diet consisting of a mixture of *P. tricornutum* and *D. euchlora*; growth of oysters exceeded that obtained with either species fed independently. In chambers containing more than 50 oysters (i.e., 100 or 200) where each population received the same amount of algal food, growth in terms of live weight was reduced in relationship to the increase in oyster population, reflecting the lower ration of algal cells available to each oyster. Nevertheless, similar peaks in live-weight relative growth were demonstrated by all three groups of oysters (Figure 3).

To test for periodicity in live-weight relative growth rate data, a matched correlation procedure was used in which correlation values were calculated for datum pairs separated by 2- to 7-week intervals (Tables 1 and 2). For oysters fed *T. pseudonana*, *D. euchlora*, or *P. tricornutum*, correlation to a 5-week period was very strong. Results suggest only a probable period of 5 weeks for the 1980 *T. maculata* data, and a weak correlation to a 6-week period for oysters fed *T. maculata* in the 1982 experiment (Table 1). Oysters in groups of 50 and 200, fed the same daily ration of a mixed suspension of *D. euchlora* and *P. tricornutum*, demonstrated a strong correlation to a 7-week cycle, but the group of 100 oysters did not conform (Table 2). Even for cases in which correlation to periodic intervals is low, the appearance of peaks in relative growth curves is remarkably consistent.

Mean shell heights for the group of 50 oysters fed the mixed algal diet are shown as both absolute and relative growth rates in Figure 4. Absolute shell growth indicated the expected slowly increasing shell height. Relative shell growth rate did not project the peaks in growth that were observed in live-weight relative growth determinations. Instead, a decrease in relative growth rate of shell height was observed similar to that described by Wilbur and Owen (1964) for shell growth in other mollusks.

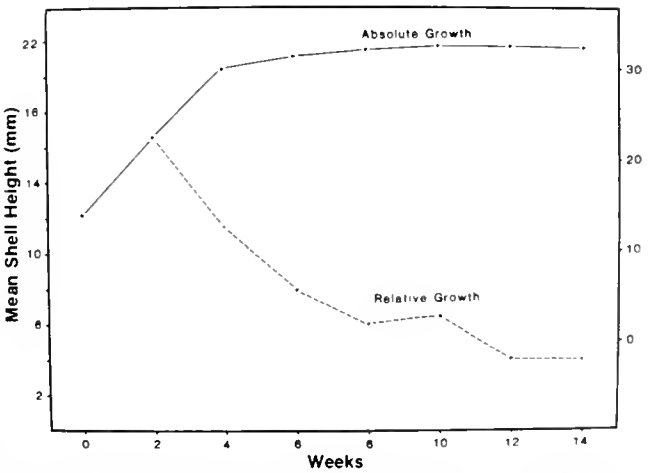


Figure 4. Absolute and relative growth of shell heights of oysters fed a mixed algal species diet.

TABLE 1.

Correlation coefficients of relative growth values compared at intervals of 2 to 7 weeks for oysters fed different algal species.

Interval (weeks)	Algal food species				
	T. maculata 1980	*T. pseudonana*	*D. euchlora*	*P. tricornutum*	*T. maculata* 1982
2	—0.18	0.03	0.33	0.51	—0.23
3	—0.14	—0.18	0.20	0.26	—0.02
4	—0.09	0.36	0.49	0.22	0.21
5	0.63*	0.97*	0.96*	0.87*	—0.20
6	0.39	0.40	0.68	0.48	—0.51*
7	0.53	—0.15	0	0.09	0.20

*Indicates interval for which correlation is highest (coefficients approaching 1 or -1 show highest correlation).

TABLE 2.

Correlation coefficients of relative growth values compared at intervals of 2 to 7 weeks for oysters fed a mixed algal species diet.

Interval (weeks)	Number of oysters in group		
	50	100	200
2	—0.40	—0.37	—0.31
3	—0.47	—0.52*	—0.17
4	—0.27	—0.26	—0.03
5	—0.07	—0.10	0.08
6	0.25	0.22	—0.02
7	0.71*	0.47	0.72*

*Indicates interval for which correlation is highest (coefficients approaching 1 or -1 show highest correlation).

DISCUSSION

Many biological processes are found to undergo cyclic changes with periods that approximate 24 hours in length; however, biological clocks that measure time in weeks, months, or years also exist, but have not been studied as often as those on a 24-hour cycle (Sweeney 1983). The present report describes a cyclic pattern of several weeks in live-weight relative growth rate of laboratory-reared juvenile oysters.

Studies of bivalve growth conducted in the natural environment are faced with a myriad of complex factors (e.g., temperature fluctuations, diurnal and tidal cycles, the sporadic or consistent introduction of pollutants to the water column, and variations in the availability of a source of food). All of these factors can obscure the interpretation of experimental results. In contrast, controlled laboratory experiments offer the opportunity to elucidate fundamental growth phenomena.

Growth data may be presented as absolute or relative growth, but in bivalve research are most often presented as absolute growth (i.e., the increase in weight or linear measurement plotted as a function of time) (Walne 1970, Epifanio et al. 1976). This method of indicating growth provides a clear visualization of cumulative size, although relative growth can be more useful in terms of the physiological response. Relative growth measurements have the advantage of expressing growth, not only per unit of time, but also per unit of weight (or length) already attained (Wilbur and Owen 1964). Relative growth rate determinations take into account the increasing size of a growing organism which may double in size in two weeks when small, but may require two months to double in size again.

The environment utilized in these experiments was kept under constant control; therefore, the peaks in relative growth rate could not be attributed to such fluctuating environmental conditions as tidal or lunar cycles. The possibility that the quality of seawater used in these experiments was affected by changes in soluble and particulate matter, and hence produced the observed growth response of experimental oysters, has been carefully considered. It has been observed that water filtered to 0.45 μm varies in the short term and seasonally according to blooms in the seawater (Michael M. Helm, Fisheries Experiment Station, Conwy, Wales; pers. comm.). It seems to us that such blooms are not likely to occur in such a short-term, repetitive manner as to coincide with the oyster growth cycles observed at different times. This contention is supported by data on *in vivo* chlorophyll fluorescence of the laboratory seawater supply before filtration (courtesy of Ronald Goldberg, NMFS, Milford, CT), collected at the same time the oyster experiments were conducted, which showed no correlation with the growth cycles observed in the oyster feeding experiments. In all experimental variables (with one exception) the peaks in relative growth occurred at 5- to 7-week intervals, although feeding was regulated to 24-hour intervals.

In the comprehensive study of feeding behavior in *C. virginica* by Higgins (1980), it was clearly shown that activity is directly related to presence of algal food. Accordingly, oysters given food at regular intervals can be expected to react by feeding in a predictable manner. The imposition

of a programmed discontinuous feeding regime in a controlled environment is likely to result in digestive rhythms which are then reflected in assimilation and, perhaps ultimately, in growth cycles. Further work will be necessary to determine which factors control the pattern of relative growth in juveniles of *C. virginica* that was observed during these studies, but we believe that the occurrence of this cyclic response is noteworthy.

ACKNOWLEDGMENT

We wish to acknowledge Dr. Michael Nabel of NRC Consultants for his contribution to the statistical analysis.

REFERENCES CITED

Andrews, J. D. 1963. Measurement of shell growth in oysters by weighing in water. *Proc. Natl. Shellfish. Assoc.* 52: 1-11.

Davis, H. C. & R. R. Guillard. 1958. Relative value of ten genera of microorganisms as foods for oyster and clam larvae. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.* 136: 293-304.

Epifanio, C. E. 1979. Growth in bivalve molluscs: nutritional effects of two or more species of algae in diets fed to the American oyster *Crassostrea virginiea* (Gmelin) and the hard clam *Mercenaria mercenaria* (L.). *Aquaculture* 18:1-12.

_____ & J. Ewart. 1977. Maximum ration of four algal diets for the oyster *Crassostrea virginiea* (Gmelin). *Aquaculture* 11:13-29.

Epifanio, C. E., C. M. Logan & C. Turk. 1976. Culture of six species of bivalves in a recirculating seawater system. Persoone, G.; Jaspers, E., eds., *Proc. 10th European Symposium on Marine Biology, Ostend, Belgium 1975;* Volume 1, Mariculture. Wetteren: Universa Press p. 97-108.

Fisher, R. A. 1938. *Statistieal Methods for Research Workers.* 7th ed. London: Oliver and Boyd.

Hawkins, A. J. S., B. L. Bayne & K. R. Clarke. 1983. Co-ordinated rhythms of digestion, absorption and excretion in *Mytilus edulis* (Bivalvia: Mollusca). *Mar. Biol. (Berl.)* 74:41-48.

Higgins, P. J. 1980. Effects of food availability on the valve movements and feeding behavior of juvenile *Crassostrea virginica* (Gmelin). 1. Valve movements and periodic activity. *J. Exp. Mar. Biol. Eeol.* 45:229-244.

Jones, D. S. 1983. Sclerochronology: reading the record of the molluscan shell. *Am. Sci.* 71:384-391.

Langton, R. W. 1977. Digestive rhythms in the mussel *Mytilus edulis. Mar. Biol. (Berl.)* 41:53-58.

_____ & P. A. Gabbott. 1974. The tidal rhythm of extracellular digestion and the response to feeding in *Ostrea edulis. Mar. Biol. (Berl.)* 24:181-187.

Mathers, N. F. 1976. The effects of tidal currents on the rhythm of feeding and digestion in *Pecten maximus* L. *J. Exp. Mar. Biol. Ecol.* 24:271-283.

Sweeney, B. M. 1983. Biological clocks - An introduction. *BioScience* 33:424-425.

Ukeles, R. 1973. Continuous culture - A method for the production of unicellular algal foods. Stein, J. R., ed. *Handbook of Phycologieal Methods - Culture Methods and Growth Measurements.* Cambridge, MA: Cambridge University Press, p. 233-254.

_____ & G. H. Wikfors. 1982. Design, construction, and operation of a rearing chamber for spat of *Crassostrea virginica* (Gmelin). *J. Shellfish Res.* 2:35-39.

Walne, P. R. 1970. Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera *Ostrea, Crassostrea, Mereenaria* and *Mytilus. Fish. Invest. Ser. II Mar. Fish. G. B. Minist. Agrie. Fish. Food* 26(5):1-62.

Wilbur, K. M & G. Owen. 1964. Growth. Wilbur, K. M.; Yonge, C. M., eds., *Physiology of Mollusca.* New York: Academic Press, Vol. I: 211-242.

Wilson, J. H. & R. W. La Touche. 1978. Intracellular digestion in two sublittoral populations of *Ostrea edulis* (Lamellibranchia). *Mar. Biol. (Berl.)* 47:71-77.

Journal of Shellfish Research, Vol. 4, No. 2, 161-163, 1984.

RESEARCH NOTE

GONADAL DEVELOPMENT AND HATCHERY REARING TECHNIQUES FOR THE MANILA CLAM *TAPES PHILIPPINARUM* (ADAMS AND REEVE)

ANJA M. ROBINSON AND WILBUR P. BREESE
Oregon State University
Department of Fisheries and Wildlife
Marine Science Center
Newport, Oregon 97365

ABSTRACT The Manila clam *Tapes philippinarum* was collected at regular intervals over a 15-mo period in the southern Puget Sound area. Histological preparations indicate that the primary spawning season for the species is from June to September. Hatchery techniques were developed for commercial production of juvenile Manila clams. Investigations of the combined effects of temperature and salinity on the growth and survival of Manila clam larvae suggest an optimum temperature of 25°C and an optimum salinity range from 20 to 30 ‰.

KEY WORDS: Manila clams, *Tapes philippinarum*, spawning cycle, hatchery techniques

INTRODUCTION

The Manila clam *Tapes philippinarum* (Adams and Reeve) (formerly *Tapes japonica* [Deshayes]) was unintentionally introduced into British Columbia and Willapa Bay and Puget Sound, Washington (Bourne 1982). Presumably this clam came with seed of the Pacific oyster *Crassostrea gigas* (Thunberg) from Japan where the Manila clam is a widely used commercial species (Bourne 1982). Manila clams now form the basis of a clam fishery along the northwest coast of North America. The high commercial value of the Manila clam has led to a desire to formulate techniques for its commercial culture. The purpose of this study was to examine the duration of the spawning season of *T. philippinarum* and develop a methodology for hatchery rearing of its larvae.

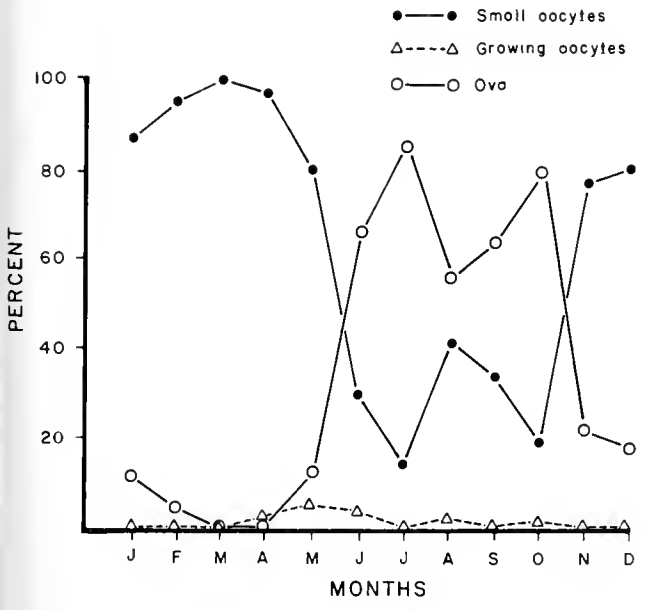


Figure 1. Annual cycle of gonadal development of females of the Manila clam *Tapes philippinarum* southern Puget Sound area (see text for details of staging technique).

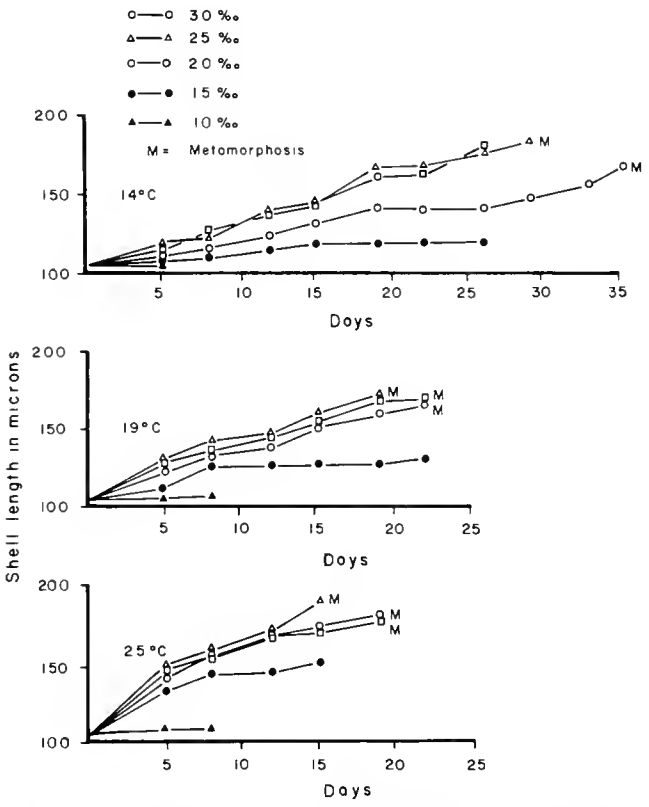


Figure 2. Relationship between salinity and shell length of larvae of the Manila clam *Tapes philippinarum* reared at three temperatures (standard deviation, Table 1).

MATERIALS AND METHODS

This study began in August 1982. Manila clams were obtained from natural population in the southern Puget Sound area. A minimum of 20 clams were collected and transported once or twice per month to the Oregon State University Marine Science Center. The sex of each clam in

spawning condition was determined by piercing the gonad and observing either the granular material containing ova from females or the milky material containing sperm from males. Approximately 1 cm^3 of gonad tissue was erased from the central part of a gonad and prepared histologically for microscopical study. The following protocol was followed: tissue was fixed in Bouin's solution for 24 hours, dehydrated in alcohol, cleared in toluene, embedded in paraffin, sectioned at 6 μ, stained in Mayer's hematoxylin, and counterstained in eosin.

The gonadal development stages were determined by staging oocytes and ova in histological sections. At least 100 oocytes and ova were counted in the follicles of each clam examined. The stages of maturation used and their respective characteristics were: (1) *Small Ooeytes*, attached to the follicle wall and staining dark purple, (2) *Growing Ooeytes*, moving from the wall of the follicle toward the lumen, club shaped with the narrow end still attached on the follicle wall, and stain lighter than small oocytes, and (3) *Fully Developed Ova* that stained pink and filled the lumen.

As clams appeared mature, spawning was attempted using *Pseudoisochrysis paradoxa* (Dupuy) as a stimulant (Breese and Robinson 1981). During a successful spawning, male and female gametes were collected in separate containers and eggs were fertilized with mixture of sperm from several males. Fertilized eggs were incubated at 18°C for 48 hours. After that period straight-hinge, veliger larvae were counted. Five-thousand larvae were distributed into each of a series of 1-l beakers filled with seawater of the following salinities 10, 15, 20, 25, and 30 ‰. Duplicate samples were reared at 14-15, 19-20 and 25°C in temperature-controlled rooms and in 10 and 30°C water baths. Larvae were fed *Pseudoisochrysis paradoxa* daily (Breese and Malouf 1975). The water in each beaker was changed on Mondays and Thursdays each week at which time the shell lengths of larvae were measured with a compound microscope equipped with a micrometer eye piece. Larvae were also examined under 40X magnification to determine the onset of metamorphosis, here defined as the appearance of the pediveliger foot and the initiating of crawling on the bottom of the beaker.

RESULTS AND DISCUSSION

The proportion of ova in the gonad of the Manila clam indicates that the most probable spawning period for this species is from June to September in the southern Puget Sound area (Figure 1). This estimated spawning time agrees with the findings of Holland and Chew (1974) and Williams (1978).

TABLE 1.

Mean shell length in microns of larvae of *Tapes philippinarum* reared at different temperatures and salinities and standard deviation. (Sample size = 20. Size of straight-hinge larvae was 105 μm.)

Temperature °C	Salinity ‰	Day-5	(SD)	Day-12	(SD)	Day-19	(SD)	Day-26	(SD)	Day-30	(SD)	Day-36	(SD)
10	10	dead											
	15	dead											
	20	dead											
	25	dead											
	30	dead											
14 ± 1	10	105	(2.7)	dead									
	15	107	(1.7)	115	(4.5)	116	(4.9)	121	(3.4)	dead			
	20	112	(3.2)	124	(5.1)	146	(8.0)	141	(7.0)	146	(8.9)	166 M[1]	(20.0)
	25	121	(2.9)	148	(8.5)	168	(12.8)	177	(15.3)	183 M[1]	(13.2)		
	30	115	(3.5)	139	(6.3)	163	(11.2)	181	(11.0)	dead			
19 ± 1	10	106	(2.6)	dead									
	15	114	(4.3)	126	(6.9)	125	(7.2)	dead					
	20	123	(4.2)	132	(8.2)	160	(14.9)	186 M[1]	(12.5)				
	25	131	(5.0)	156	(13.5)	174 M[1]	(11.8)						
	30	130	(3.9)	148	(10.4)	168	(12.4)	176 M[1]	(12.5)				
25 ± 1	10	109	(2.6)	dead									
	15	134	(5.0)	143	(14.2)	dead							
	20	143	(5.4)	168	(14.8)	181 M[1]	(13.9)						
	25	150	(4.2)	171	(17.8)	196 M[1]	(13.8)						
	30	147	(7.9)	159	(17.7)	177 M[1]	(14.4)						
30	10	dead											
	15	dead											
	20	dead											
	25	dead											
	30	dead											

[1](M = metamorphosis)

The larvae of the Manila clam metamorphosed at shell lengths of 165 to 180 μm. Time to metamorphosis was dependent upon temperature and salinity (Figure 2). At 25 ± 1°C and 20-30 ‰ larvae metamorphosed in 19 days, whereas at 14 ± 1°C and 20-25 ‰ 29 or more days were required. At 19 ± 1°C and 20-30 ‰ 19 to 22 days passed before any pediveligers were observed. No larvae survived at the experimental temperatures of 10 and 30°C (Table 1). In low salinities of 10 and 15 ‰ larval growth was slow in all temperatures and larvae did not survive to metamorphosis. Also, at 30 ‰ and 14 ± 1°C all larvae died before metamorphosis. Optimal growth and survival conditions for the larvae of the Manila clam occurred at a temperature of 25 ± 1°C and a salinity range of 20 to 30 ‰. The optimum salinity for growth and survival over the temperature range from 14 to 25°C was 25 ‰. These combinations of temperature and salinity the hatchery procedures described in the hatchery manual for the Pacific oyster larvae (Breese and Malouf 1975) can be used successfully to culture Manila clam larvae.

Juvenile Manila clams, produced by using the techniques described here, have been planted in Tillamook Bay. Although more comprehensive field studies on survival are necessary, it appears that this species can be cultured successfully to market size (see Anderson et al. 1982). Commercial hatchery production of Manila clam seed may then enhance clam production in the Pacific Northwest.

ACKNOWLEDGMENTS

We express our sincere appreciation to Fowler's Yaquina Pacific Oyster Company for their efforts in supplying monthly samples of Manila clams for this study from southern Puget Sound area.

This publication is the result, in part, of research sponsored by NOAA Office of Sea Grant, Department of Commerce, under Grant No. NA81AA-D-00086 (Project No. A/Aq-44). The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon. Oregon Agricultural Experiment Station Technical Paper No. 7136.

REFERENCES CITED

Anderson, G. J., M. B. Miller & K. K. Chew. 1982. A guide to Manila clam aquaculture in Pugent Sound, Washington. Seattle, WA: *Univ. Wash. Sea Grant Prog. Publ.* No. WSG-82-4:45 pp.

Bourne, Neil. 1982. Distribution, reproduction and growth of Manila clam, *Tapes philippinarum* (Adams and Reeve) in British Columbia. *J. Shellfish Res.* 2(1):47-54.

Breese, W. P. & R. E. Malouf. 1975. Hatchery manual for the Pacific oyster. *Oreg. State Univ. Sea Grant Col. Prog.* Publ. ORESU-H-75-002: 22 pp.

Breese, W. P. & A. M. Robinson. 1981. Razor clams *Siliqua patula* (Dixon), gonadal development, induced spawning and larval rearing. *Aquaculture* 22:27-33.

Holland, D. A. & K. K. Chew. 1974. Reproductive cycle of the Manila clam *Venerupis japonica* from Hood Canal, Washington. *Proc. Natl. Shellfish. Assoc.* 64:53-58.

Williams, J. G. 1978. The influence of adults on the settlement, growth and survival of spat in the commercially important clam, *Tapes japonica* Deshayes. Seattle, WA: Univ. of Washington. Available from: University Microfilms, Ann Arbor, MI; Publ. No. 78-20, 786. 70 p. Dissertation.

Journal of Shellfish Research, Vol. 4, No. 2, 165-166, 1984.

RESEARCH NOTE

SPAWNING CYCLE OF THE WEATHERVANE SCALLOP *PECTEN (PATINOPECTEN) CAURINUS* GOULD ALONG THE OREGON COAST

ANJA M. ROBINSON
WILBUR P. BREESE
Oregon State University
Department of Fisheries and Wildlife
Marine Science Center
Newport, Oregon 97365

ABSTRACT The annual spawning cycle of the weathervane scallop *Pecten (Patinopecten) caurinus* was estimated from histological preparations of gonadal tissues obtained from natural populations. Spawning occurs from mid-January to June along the Oregon coast.

KEY WORDS: gametogenesis, Pecten, scallop, spawning cycle.

INTRODUCTION

The Pacific weathervane scallop *Pecten* (subgenus *Patinopecten) caurinus* Gould occurs along the west coast of North America from south Alaska to San Francisco (Mottet 1979). In Alaska, commercial quantities are reported to exist only around Kodiak and Yakutat (Haynes 1968). Ronholt and Hitz (1968) and Hennick (1970) reported that populations off the Oregon coast were insufficient to support commercial exploitation; however, in 1981 large commercial beds of *P. caurinus* located off Coos Bay, OR, attracted East Coast fishermen. By the year's end, 7.6 x 10^3 MT, nearly twice the 1981 Alaskan harvest, (R. Kaiser, Oregon Dep. Fish and Wildlife, Newport, OR; pers. comm., 1983) were harvested from off the Oregon coast (Starr and McCrae 1983). The scallop beds were depleted in one year and the commercial exploitation of the species has substantially decreased. The Oregon Department of Fish and Wildlife implemented a sampling program to gather information on size and age distribution of *P. caurinus*. Here we report on examination of samples of gonad tissue from natural populations that were examined to determine the annual spawning cycle of *P. caurinus* in Oregon.

MATERIALS AND METHODS

Weathervane scallops were obtained from commercial catches along the Oregon coast from March 1981 through December 1983. Although primarily from Coos Bay beds, scallops were collected off Yaquina Head, Tillamook, and Astoria. Samples of 20 to 50 live scallops were collected once or twice monthly. Scallop gonads were removed, preserved in Bouin's solution, and brought to Oregon State University's Marine Science Center. Approximately 1-cm^3 tissue samples were excised from each gonad, dehydrated in alcohol, cleared in toluene, embedded in paraffin, and sectioned at a thickness of 6 microns. Tissue sections were mounted, stained with hemotoxylin, and counterstained with eosin (Lannan 1980).

Sex and maturity of the gametes were determined by microscopic examination of histological preparations. Female gonadal development was determined by staging at least 100 oocytes and ova in the discrete follicles seen in histological sections. The stages of oocyte maturation used and their respective characteristics were: 1) *Small Oocytes*, dark staining, synaptic cells; 2) *Growing Oocytes*, light staining often club shaped cells which extend from the wall of the follicle toward the lumen; 3) *Fully Developed Ova*, pink staining, fully developed oocytes filling the lumen of the follicle. Male gonads were examined for evidence of transformation of spermatocytes on the walls of the follicle into the mature spermatozoa filling the lumen.

RESULTS AND DISCUSSION

The sex ratio of this dioecious species was 1:1. No hermaphrodites were observed. Color and size of gonads varied greatly throughout the breeding season. Gonads were largest and most intense in color just before spawning. Sex of a scallop in spawning condition was easily determined; male gonads were creamy white whereas female gonads were orange-red.

No significant differences in spawning times were found between the samples from different locations along the Oregon coast and data were pooled for each calendar month to obtain a sample size of approximately 100 gonads. Microscopic observations of histologically prepared male gonads showed ripe sperm in the follicles about 2 weeks before the first ova in female gonads appeared. Also, sperm remained in the male follicles after most ova in the female gonads had been spent.

The annual pattern of gonadal development observed in female weathervane scallops showed the percent of ova to be lowest from July through September (Figure 1). In late September the number of ova began to increase. By the beginning of January the follicles were filled with ova and scallops appeared ready to spawn. In mid-January, of 97 scallops collected, 10 females and 9 males had spawned, indicating that about 20% of the population was in process of

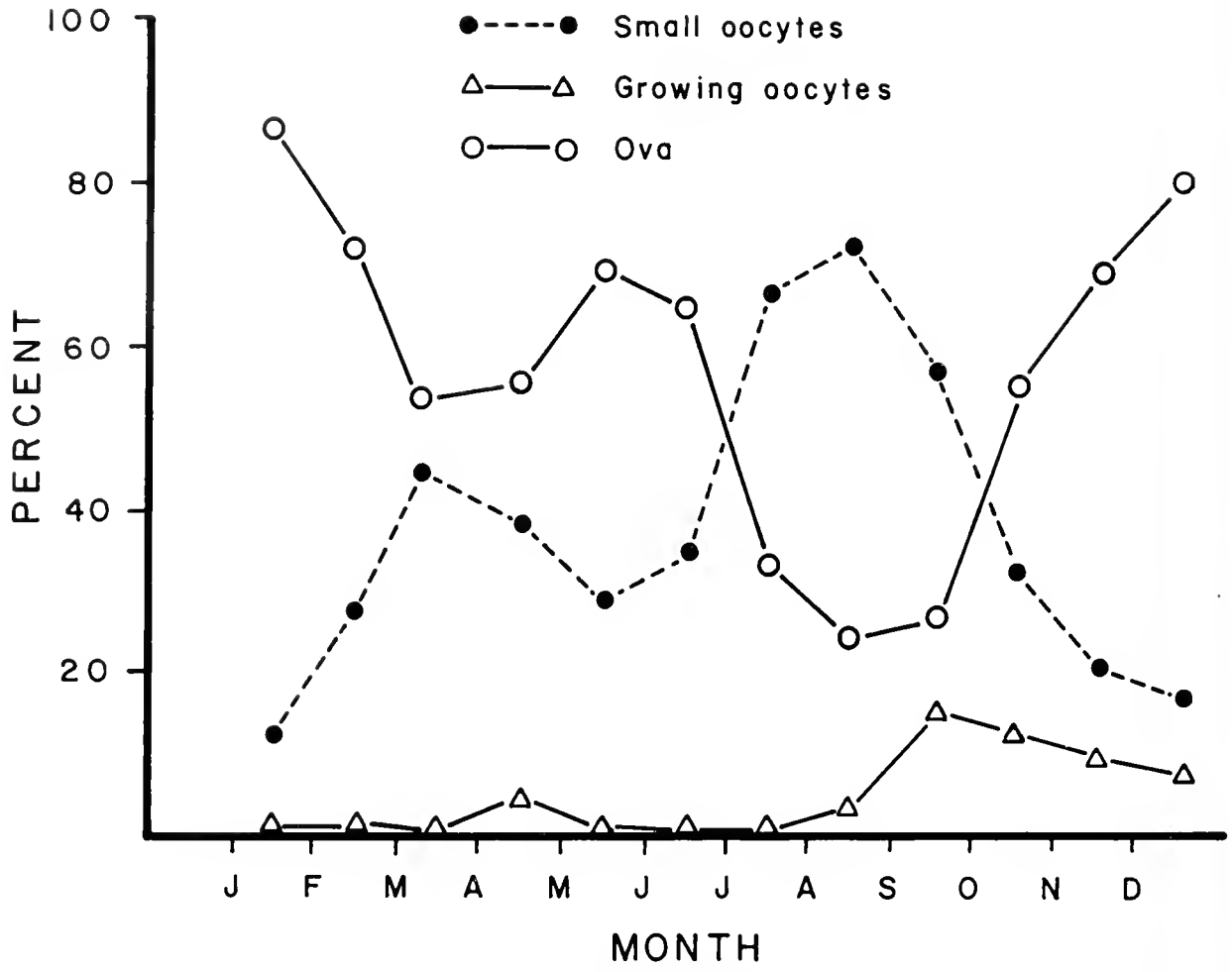


Figure 1. Annual cycle of gonadal development of the female of *Peeten caurinus* on the Oregon coast.

spawning or had spawned. In early February, of 91 scallops collected, 13 females and 17 males had spawned, indicating that approximately 33% of population was spawning or had spawned. The percents of partially spawned scallops in March, April, and May samples were between 30 and 40% and during the first half of June spawned individuals consisted of 58% of the sample. The percentages of spawning scallops indicate that the population of Oregon weathervane scallops has one primary spawning season extending from mid-January through June. In Alaska, the weathervane scallops develop ripe gonads by mid-January but spawning is delayed until June and July (Hennick 1970). Thus, actual spawning begins about four months earlier in Oregon than in Alaska.

ACKNOWLEDGMENTS

This work was supported by NOAA under Contract 80-ABH-00043. Technical Paper Number 6432 Oregon Agricultural Experiment Station.

REFERENCES CITED

Haynes, Evan B. 1968. A preliminary report on the Alaska sea scallop fishery exploration, biology and commerical processing. *Alaska Dep. Fish Game Info. Leaf.* 125:20 pp.

Hennick, D. P. 1970. The weathervane scallop fishery of Alaska with notes on occurrence in Washington and Oregon. *Pac. Mar. Fish. Comm. Annu. Rep.* 22:33-34.

Lannan, James E. 1980. Broodstock management of *Crassostrea gigas*. I. Genetic and environmental variation in survival in the larval rearing system. *Aquaculture* 21:323-336.

Mottet, Madelon Green. 1979. A review of the fishery biology of scallops. *Wash. Dep. Fish. Tech. Rep.* 39:100 pp.

Ronholt, L. L., Hitz, C. R. 1968. Scallop exploration off Oregon. *U. S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* 30(7):42-49.

Starr, R. M. & J. E. McCrae. 1983. Weathervane scallop *(Patinopecten caurinus)* investigations in Oregon 1981-1983. *Oreg. Dep. Fish. Wildl. Info. Rep.* 83-10:55 pp.

INFORMATION FOR CONTRIBUTORS TO THE *JOURNAL OF SHELLFISH RESEARCH*

Original papers dealing with all aspects of shellfish research will be considered for publication. Manuscripts will be judged by the editors or other competent reviewers, or both, on the basis of originality, content, merit, clarity of presentation, and interpretations. Each paper should be carefully prepared in the style followed in Volume 3, Number 1, of the *Journal of Shellfish Research* (1983) before submission to the Editor. Papers published or to be published in other journals are not acceptable.

Title, Short Title, Key Words, and Abstract: The title of the paper should be kept as short as possible. Please include a "short running title" of not more than 48 characters including space between words, and approximately seven (7) key words or less. Each manuscript must be accompanied by a concise, informative abstract, giving the main results of the research reported. The abstract will be published at the beginning of the paper. No separate summary should be included.

Text: Manuscripts must be typed double-spaced throughout one side of the paper, leaving ample margins, with the pages numbered consecutively. Scientific names of species should be underlined and, when first mentioned in the text, should be followed by the authority.

Abbreviations, Style, Numbers: Authors should follow the style recommended by the fourth edition (1978) of the *Council of Biology Editors [CBE] Style Manual*, distributed by the American Institute of Biological Sciences. All linear measurements, weights, and volumes should be given in metric units.

Tables: Tables, numbered in Arabic, should be on separate pages with a concise title at the top.

Illustrations: Line drawing should be in black ink and planned so that important details will be clear after reduction to page size or less. No drawing should be so large that it must be reduced to less than one third of its original size. Photographs and line drawings preferably should be prepared so they can be reduced to a size no greater than 17.3 cm X 22.7 cm, and should be planned either to occupy the full width of 17.3 cm or the width of one column, 8.4 cm. Photographs should be glossy with good contrast and should be prepared so they can be reproduced without reduction. Originals of graphic materials (i.e., line drawings) are preferred and will be returned to the author. Each illustration should have the author's name, short paper title, and figure number on the back. Figure legends should be typed on separate sheets and numbered in Arabic.

No color illustrations will be accepted unless the author is prepared to cover the cost of associated reproduction and printing.

References Cited: References should be listed alphabetically at the end of the paper. Abbreviations in this section should be those recommended in the *American Standard for Periodical Title Abbreviations*, available through the American National Standards Institute, 1430 Broadway, New York, NY 10018. For appropriate citation format, see examples at the end of papers in Volume 3, Number 1, of the *Journal of Shelfish Research* or refer to Chapter 3, pages 51—60 of the *CBE Style Manual.*

Page Charges: Authors or their institutions will be charged $25.00 per printed page. If illustrations and/or tables make up more than one third of the total number of pages, there will be a charge of $30.00 for each page of this material (calculated on the actual amount of page space taken up), regardless of the total length of the article. All page charges are subject to change without notice.

Proofs: Page proofs are sent to the corresponding author and must be corrected and returned within seven days. Alterations other than corrections of printer's errors may be charged to the author(s).

Reprints: Reprints of published papers are available at cost to the authors. Information regarding ordering reprints will be available from the National Shellfisheries Association at the time of printing.

Cover Photographs: Particularly appropriate photographs may be submitted for consideration for use on the cover of the *Journal of Shellfish Research*. Black and white photographs, if utilized, are printed at no cost. Color illustrations may be submitted but all costs associated with reproduction and printing of such illustrations must be covered by the submitter.

Corresponding: An original and two copies of each manuscript submitted for publication consideration should be sent to the Editor, Dr. Roger Mann, The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

JOURNAL OF SHELLFISH RESEARCH

Vol. 4, No. 2 December 1984

CONTENTS