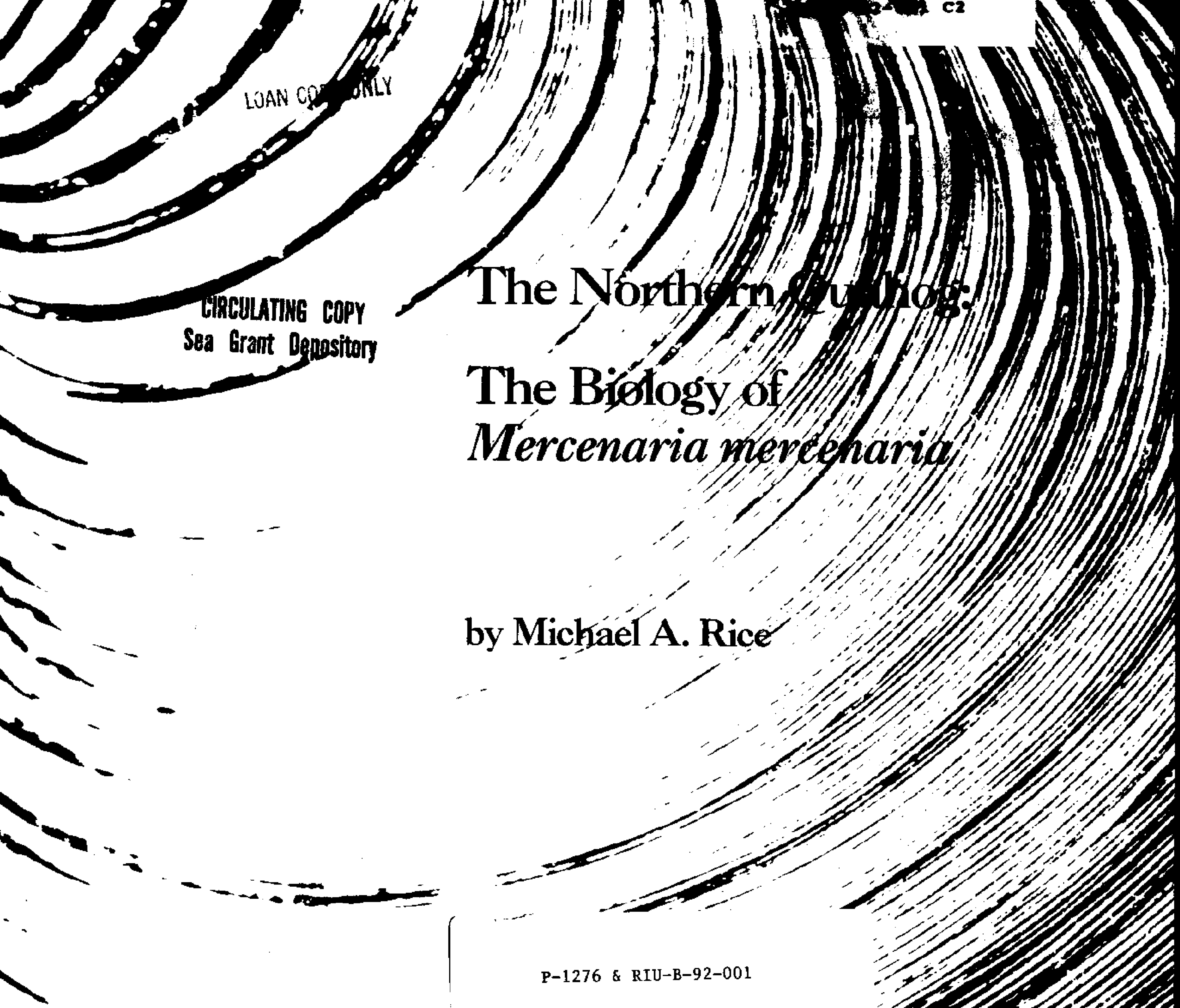

# The Northern Quahog:

## The Biology of *Mercenaria mercenaria*

by Michael A. Rice

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# The Northern Quahog:

# The Biology of *Mercenaria mercenaria*

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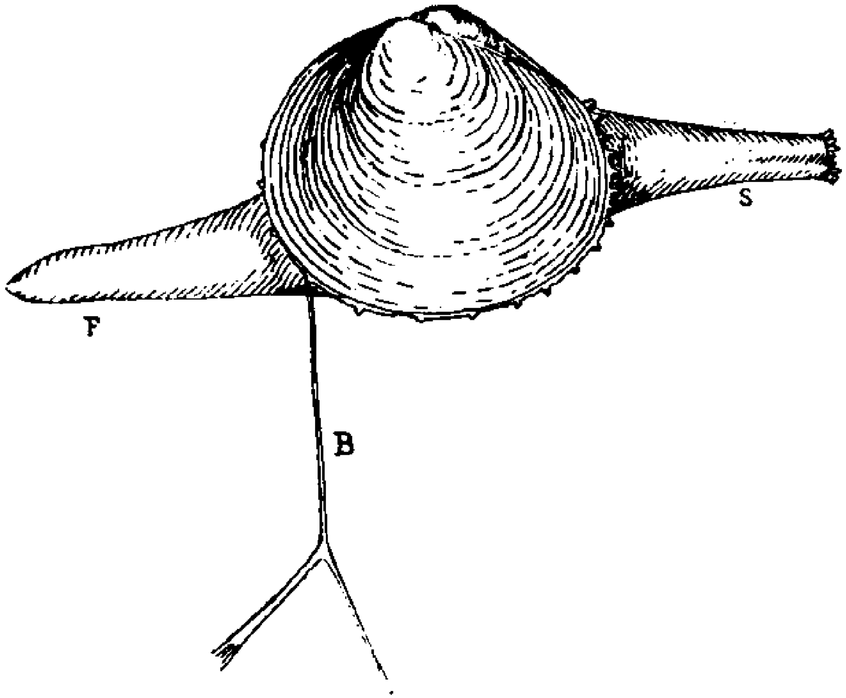


Drawn from living clam .04mm (less than one-fiftieth of an inch) in length. S, siphons, two tubes, one of which conducts water bearing food and oxygen to the body within the shell, the other conducting a stream containing waste matter to the exterior. F, foot, the organ of locomotion. B, byssus, a delicate thread for attachment, which is not present in the adult. *From Bulletin of the New York State Museum, No. 43, Vol. #8. April 1901.*

# Contents

# Acknowledgements

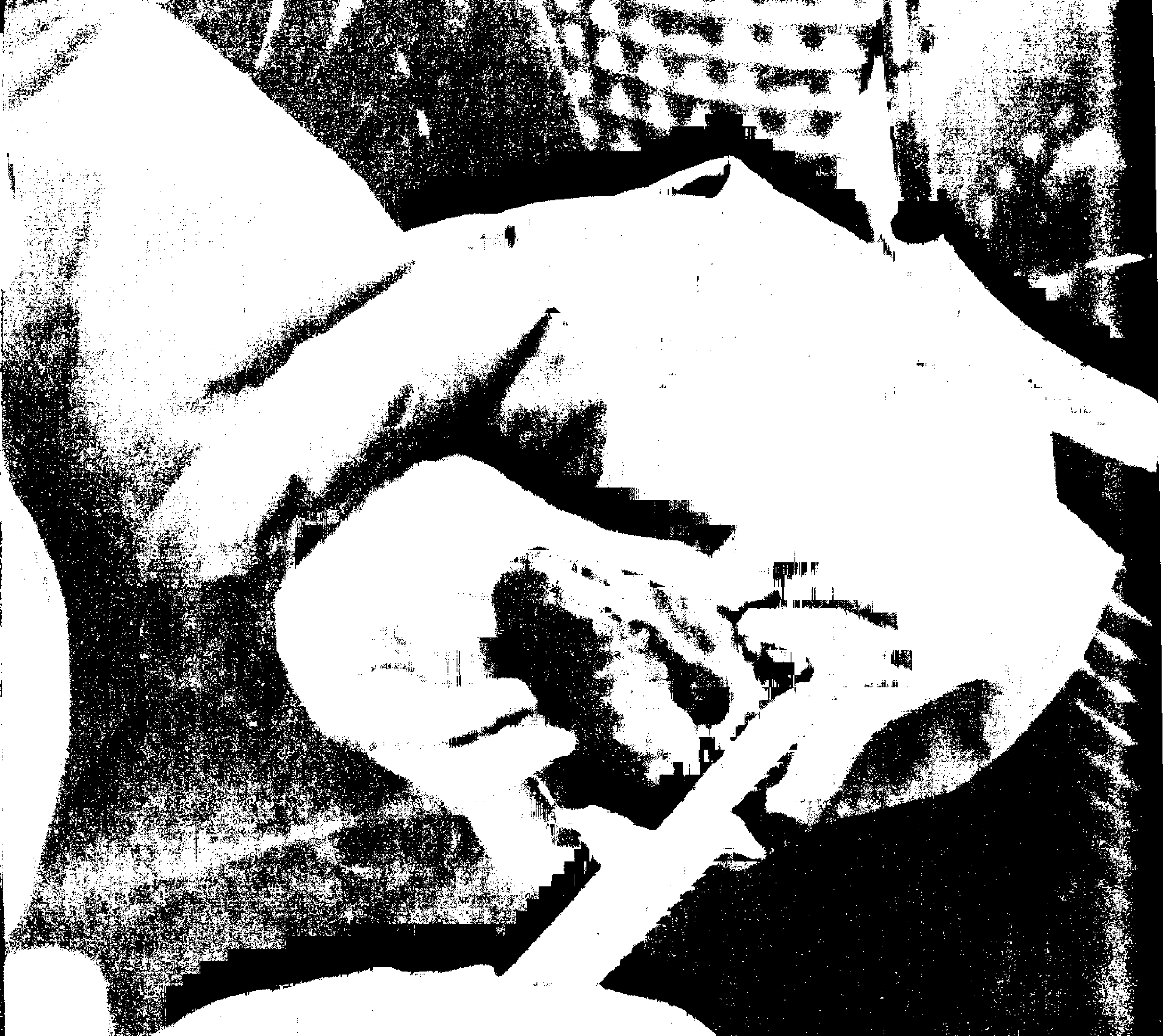
I wish to acknowledge a number of individuals and organizations who were very helpful in the production of this book. Elizabeth Watkins and Vincent Encena provided many of the line drawings. Recognition is due to William Brown Publishers, Macmillan Publishers, the *Journal of Shellfish Research, Transactions of the American Fisheries Society,* and *Scientific American* for granting permission to reproduce previously published material. I especially thank Dr. Joseph DeAlteris, Dr. Lindy Eyster, Dr. Jan A. Pechenik, Dr. Conrad Recksiek, Ms. Kathleen Castro, Mr. Gef Flimlin, Ms. Carole Jaworski, and Mr. Robert Rheault for providing valuable comments on the manuscript.

*Photograph by Donna Palumbo O'Neill*

# Introduction

The northern quahog, *Mercenaria mercenaria* (Linnaeus), is of interest to many people, especially to those living along the eastern seaboard of the United States. This species supports valuable commercial and recreational shellfisheries all along the Atlantic coast. Seafood connoisseurs enjoy a host of delectable recipes all dependent on its delicate flavor. In addition, some marine scientists find the quahog to be the ideal organism to study a host of fundamental scientific problems. The importance of the quahog to many people has not been overlooked by the legislature of the state of Rhode Island, which designated the quahog as the official state mollusk.

This book is patterned after a previous Rhode Island Sea Grant publication on the lobster (J. Stanley Cobb's (1976) *The American Lobster: The Biology of* Homarus americanus) and is intended to be a companion volume. The aim of this book is to provide an overview of some of the information available about the quahog, and to provide a starting point for those who wish to delve further into the *Mercenaria* literature. Although the references section of this book contains a number of recent citations, the serious researcher should be aware of an excellent annotated bibliography (174) containing over 2,200 citations.



# General Biology

# 1

## Taxonomic Position and Common Names

*Mercenaria mercenaria* (Linnaeus, 1758) is a mollusk of the class Bivalvia (formerly Pelecypoda), subclass Lamellibranchiata, order Heterodonta, and family Veneridae. Thus, its shell has two valves, it has sheet-like gills, it is clam-like with large hinge teeth, and is in the family of hard-shelled clams. In the literature prior to the early 1960s, the quahog is known as *Venus mercenaria* L., 1758. The accepted official malacological common name (the name used by molluskan scientists and shell enthusiasts) for *M. mercenaria* is the northern quahog, but it is locally known as hard clam, hard-shell clam, round clam, or quahog (quahaug). In addition to these regional names, there are different names for animals of different sizes. In Rhode Island, the smallest legally sold quahogs (approximately 48 millimeters valve length) are known as "littlenecks." Intermediate-sized (>60mm length) and large (>75mm length) are known as "cherrystones" and "chowder quahogs," respectively. In some other localities, the term "cherrystone" refers to the smallest animals that can be legally harvested. Other market names include "topnecks" and "topcherries" for intermediate-sized animals.

In New England, quahogs have been harvested since pre-colonial times. According to the *Oxford English Dictionary*, Roger Williams, the first colonial governor of the Providence Plantation Colony, wrote in 1643, "Poquauhock, this the English call Hens, a little thick shel-fish (sic), which the Indians wade deepe (sic) and dive for." Our modern word "quahog" is derived from "poquauhock" in the language of the Narragansett Indians (living in what is now Rhode Island). They ate the meat and used the shells to make wampum beads, which were a trading currency. The wampum beads made from the

***Photograph by Michael A. Rice***

purple shell margins were especially valuable. Indeed, the species name "*M. mercenaria*" refers to their former value as a trading currency.

## Geographic Distribution and Recognized Subspecies

The quahog inhabits shallow coastal waters from The Gulf of St. Lawrence in Canada to Florida (181). It has been introduced into Europe (7; 115; 116; 117) and California (45; 56). One recognized subspecies is *Mercenaria mercenaria notata*, which is characterized by chestnut-colored, often chevron-shaped markings on the shell exterior (52; 96). Field and laboratory studies suggest that the *M. m. notata* subspecies occurs with a frequency of 1 to 2 percent or less in the southern Atlantic states (76; 120). The subspecies *Mercenaria mercenaria texana* is native to the northern coast of the Gulf of Mexico (1; 55).

## Similar Bivalve Species

The southern quahog, *Mercenaria campechiensis*, is a closely related species that has more prominent shell sculpturing and attains larger sizes. *M. campechiensis* is found in the more southern regions of the range of *M. mercenaria* and the two species are reported to form hybrids (68; 176). The false quahog, *Pitar morrhuanus* (formerly *Callocardia*), is found in the geographic range of *M. mercenaria* (96). Individuals of the false quahog, *P. morrhuanus*, reach a maximum size of about 60mm valve length, have thinner shells than *Mercenaria*, and are dull gray with smoother shells. There is evidence that *Pitar* prefers a muddier substrate than does *Mercenaria* (200).

## Anatomy

The quahog, like all other clams, has its soft tissues surrounded by a shell consisting of two halves or valves. The quahog shell consists of calcium carbonate in a crystalline form (aragonite) held in a network of complex organic molecules (105). The valves are held together by a tough, but pliable, hinge ligament along the top or dorsal section of the animal, called the hinge plate. The valve hinge, which consists of intermeshing teeth, forms the joint between the valves. The hinge allows for opening and closing of the shell. In close proximity to the hinge is the umbo—or what is commonly known as the "beak." If you note the roughly triangular shape of the quahog, and orient the quahog so that the hinge and the umbo are at the top or dorsal, the widest edge of the shell—or the part that is opposite the umbo—is the ventral shell margin. The umbo is the oldest section of the shell, with subsequent shell growth radiating out from it. The concentric rings on the external surface of

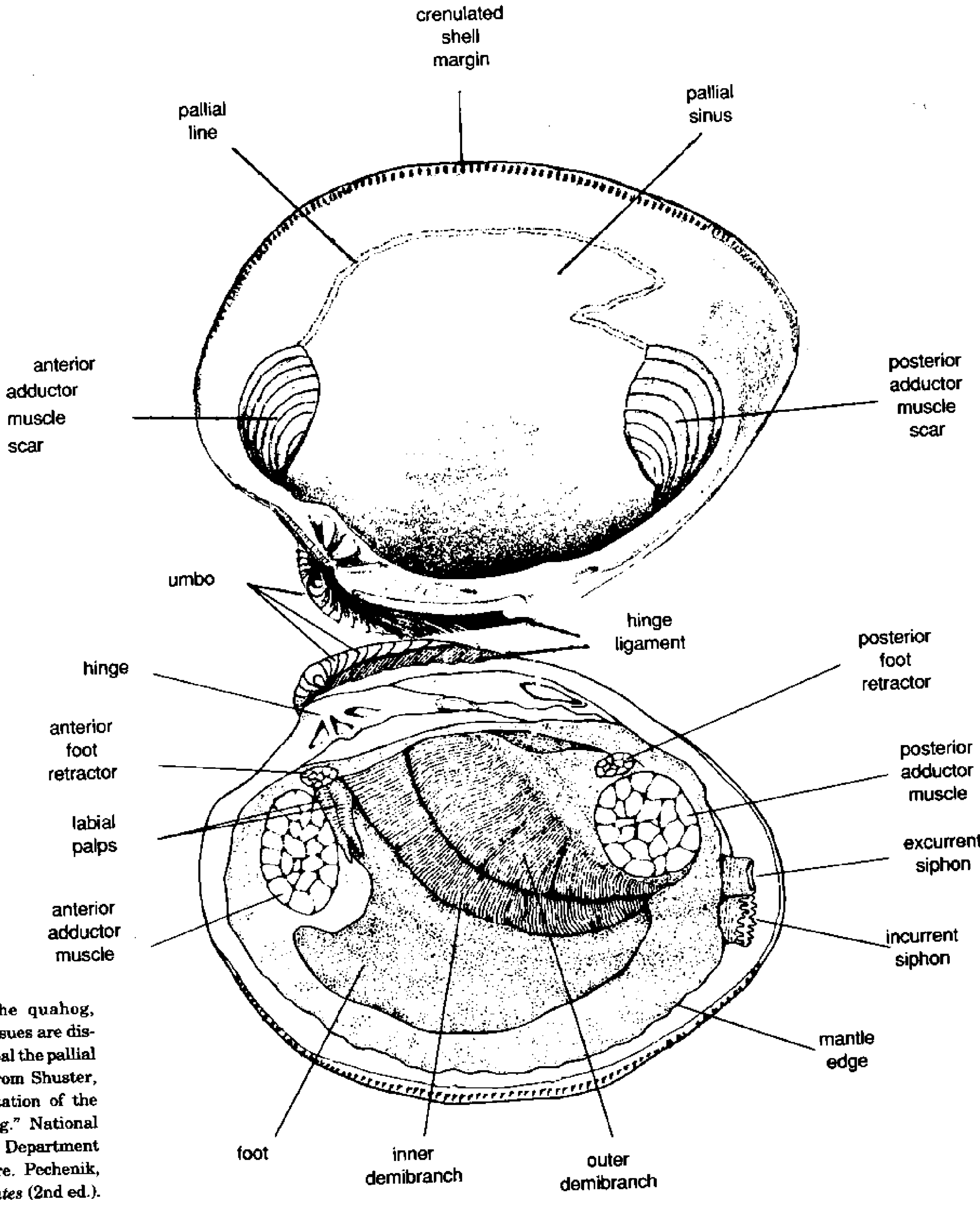


**Figure 1.** Gross anatomy of the quahog, *Mercenaria mercenaria*. The soft tissues are dissected free from the left valve to reveal the pallial line and adductor muscle scars. From Shuster, C.N. 1966. "A three-ply representation of the major organ systems of a quahog." National Shellfish Sanitation Program, U.S. Department of Health, Education, and Welfare. Pechenik, J.A. 1991. *Biology of the Invertebrates* (2nd ed.). William C. Brown Publishers. Used with permission.

the shell indicate the general growth pattern of the animal. The mantle is responsible for the formation of new shell material. New shell forms at the ventral shell edge by secretion of the network of organic molecules (proteinaceous matrix) and calcium carbonate by the mantle (185; 248; 254; 255). The extrapallial fluid (EPF) is a liquid similar to seawater and the blood of the quahog and is found between the mantle and shell. This fluid plays an important role in the shell formation process (57). Features associated with the inner surfaces of the shell include the pallial line, which is the point of attachment for the mantle. Muscle scars are the depressions near the front (anterior) and rear (posterior) ends of the valves. These muscle scars are the points of attachment for the posterior and anterior adductor muscles (Fig. 1).

The valves are closed by the posterior and anterior adductor muscles. The primary function of the two adductor muscles is to keep the valves closed in response to predators or adverse environmental conditions. In each of the adductor muscles there are two fiber types arranged in distinct regions of the muscle. These regions are pinkish in color for the fast fibers and white for the catch muscle fibers. The fast muscle is responsible for the rapid closure of the shell; its pinkish color reflects the presence of a pigmented, iron-containing protein called myoglobin (138). The function of myoglobin is to bind and store oxygen from the blood and release it as the muscle requires more oxygen for metabolic activity. Catch muscles can maintain the shells in a closed position for long periods of time with little or no fatigue (11; 53; 157).

A large muscular foot that can be extended beyond the ventral shell margin allows for burrowing (Fig. 1). Key muscles controlling the foot are the anterior and posterior foot retractor muscles and the muscles of the foot itself. These allow for rapid retraction of the extended foot and locomotion both vertically and horizontally in the sediments.

Other key features of the gross anatomy of a quahog include the incurrent (incoming water) and excurrent siphons (outgoing water) (Fig. 1). The incurrent and excurrent siphons have sometimes been called "necks." Since quahogs are normally buried in the sediments, the siphons extend into the water column above, so that water can be taken into and expelled by the animal. The water brought into the quahog via the incurrent siphon contains oxygen for respiration and tiny food organisms. Metabolic wastes are expelled in the out-flowing water of the excurrent siphon. Lateral cilia (microscopic hair-like appendages) on the filaments of the gills act to propel the water through the animal (108; 129). The gills act to filter out food particles in the incurrent water and provide a surface for gas exchange. Labial palps at the anterior section of the gills provide for food sorting prior to ingestion via the mouth. Details of filter feeding and gas exchange will be discussed later.

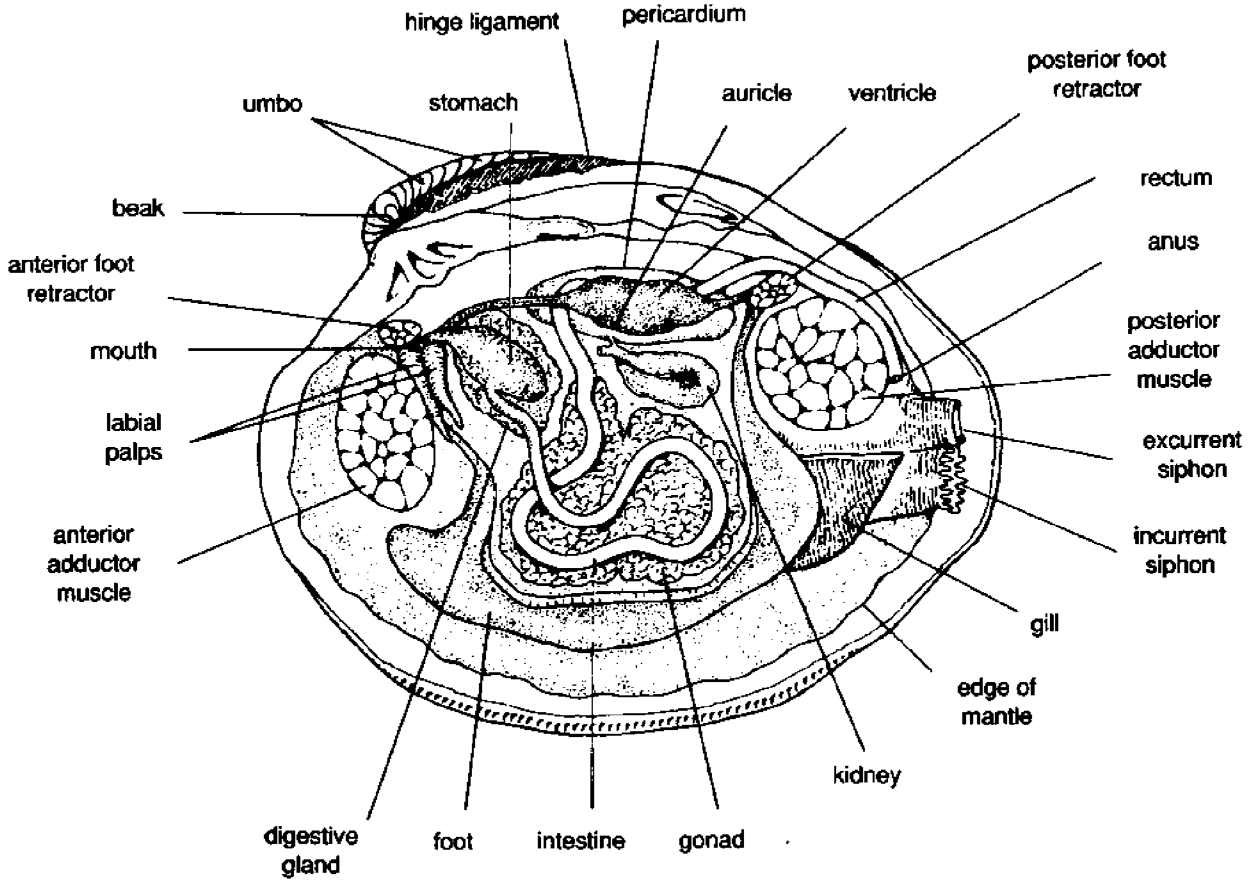
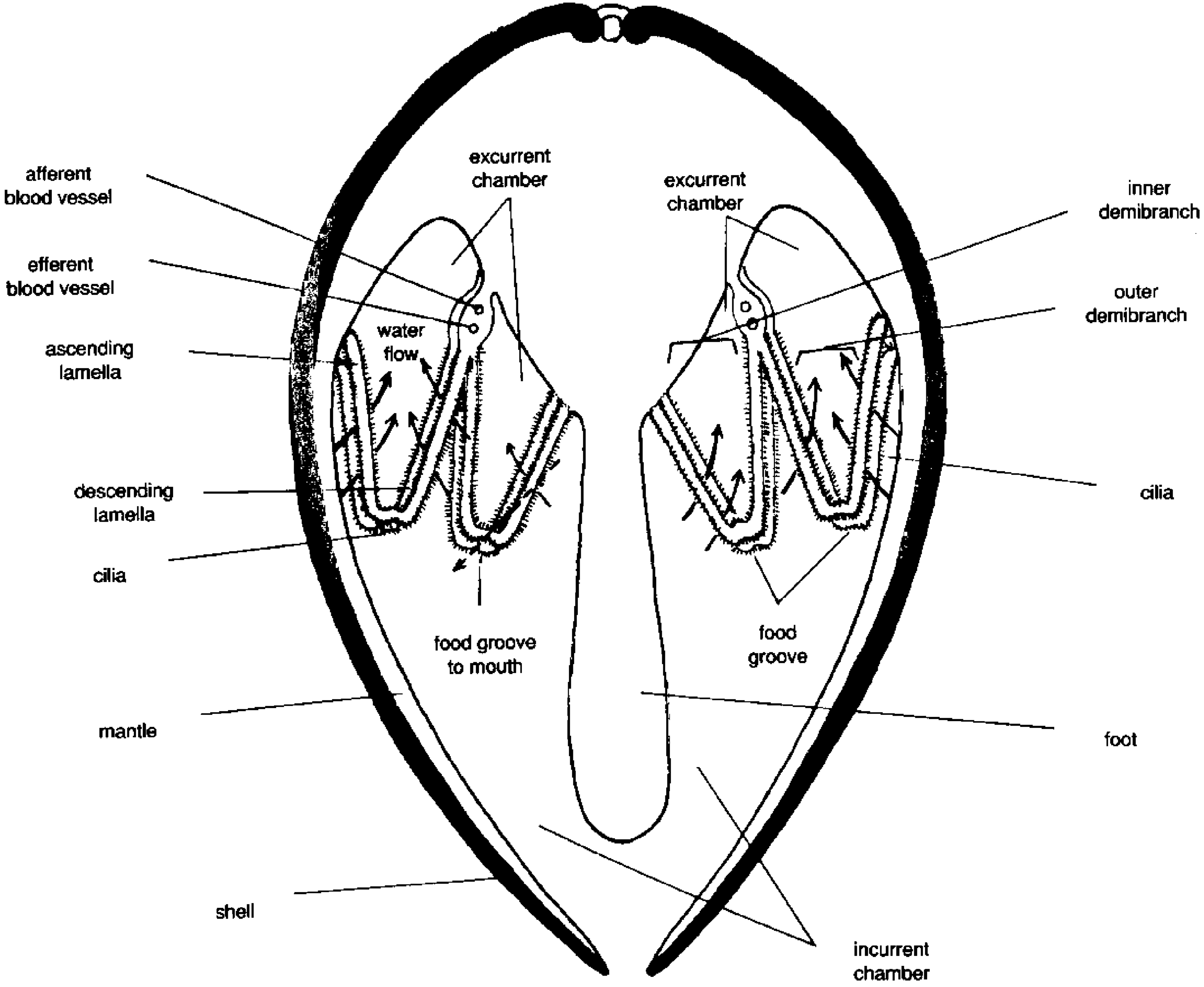


**Figure 2.** Diagrammatic representation of the major organ systems in the visceral mass of the quahog, *Mercenaria mercenaria*. Pechenik, J.A. 1991. *Biology of the Invertebrates* (2nd ed.). William C. Brown Publishers. Used with permission.

Most of the digestive, circulatory, excretory, and reproductive organs are contained within the major body mass (visceral mass) lying above the foot (Fig. 2). A two-chambered heart is surrounded by a fluid-filled sac called the pericardium. Closely associated with the pericardium is the kidney. The digestive system consists of a short esophagus leading to the stomach. Leaving the stomach, the intestine passes through extensive gonadal tissue and then dorsally through the heart. The rectum is situated in a position above the posterior adductor muscle. The anus opens into a chamber that leads directly to the excurrent siphon (Fig. 2).

## Respiration and Circulation

Water is drawn by gill cilia into the quahog through the incurrent siphon and passed across the gills, which provide a surface for gas exchange (Fig. 3). There may also be considerable gas exchange across the mantle surface of bivalves (84; 85). Blood vessels within the gills provide a means for transporting oxygen to sites of metabolic need. The blood, called hemolymph, is


afferent blood vessel
efferent blood vessel
ascending lamella
descending lamella
cilia
mantle
shell
excurrent chamber
water flow
food groove to mouth
excurrent chamber
inner demibranch
outer demibranch
cilia
food groove
foot
incurrent chamber

delivered by the arterial system from the heart to the gills, where oxygen is picked up, and then transported to the outer tissues. The quahog has an open circulatory system so once in the outer tissues, the hemolymph is released from the blood vessels into open sinuses to directly bathe the tissues and to deliver oxygen. The hemolymph passes through the kidney as it returns toward the heart and collects in the open space of the pericardium. It is then drawn into the two chambers of the heart to start the circulatory cycle over again. The hemolymph of quahogs does not carry any specialized proteins (respiratory pigments) to aid in the transfer of oxygen. Gasses are dissolved directly in the hemolymph. The hemolymph is chemically similar to, but not identical to, the extrapallial fluid (57; 209).

## Filter Feeding and Digestion

The process of food acquisition by the quahog is dependent on the pumping of water (249) (Fig. 3). As water passes between the gill filaments, particulate matter, such as silt and phytoplankton, is trapped on mucous sheets on the outer surface of the gills (21). Specialized cells in the gill are responsible for the production of the large quantity of mucous necessary for trapping food particles in the internal water stream. The filtration efficiency (the amount of particles retained per unit volume of water pumped) of quahog gills is known to decrease as particle concentration in the water increases (245). This decrease in filtration efficiency serves to regulate the amount of food available to be passed along to the digestive tract. Frontal cilia along the outer surface of the gill move all trapped particulate material (food as well as non-food items such as silt) in the mucous to food grooves (ciliated tracts similar to a conveyer belt) at the ventral edge of each of the gills (Fig. 3). Once the particulate matter trapped in mucous reaches the food groove, it is carried along by ciliary motion anteriorly toward the labial palps and mouth. The labial palps act to sort and further regulate the amount of food ingested (24). Rejected particulate matter, such as silt or excess phytoplankton, is dropped onto the mantle surface, eventually to be released as mucous-coated balls resembling feces (pseudofeces) (32).

**Figure 3.** Diagrammatic mid-body transverse section of a lamellibranch bivalve showing the position of the gills and water flow during active pumping and particle filtration. From Russell-Hunter, W.D. 1979. *Life of the Invertebrates.* Macmillan Publishing Company. Used with permission.

Ingested food particles are passed through the mouth and esophagus to a multi-chambered stomach with numerous passageways and dead-end sacs (digestive diverticula) (203). One of the key organs associated with the stomach of the quahog is the crystalline style, a thin glass-clear organ that is often mistaken for a worm, but actually contains digestive enzymes. The style is located in the style sac, which is close to the stomach. During digestion, the style is rotated by cilia located along the walls of the style sac to release digestive enzymes and natural "detergents" (emulsifiers), which aid in the digestion of fats (204; 221). The style may also have a grinding

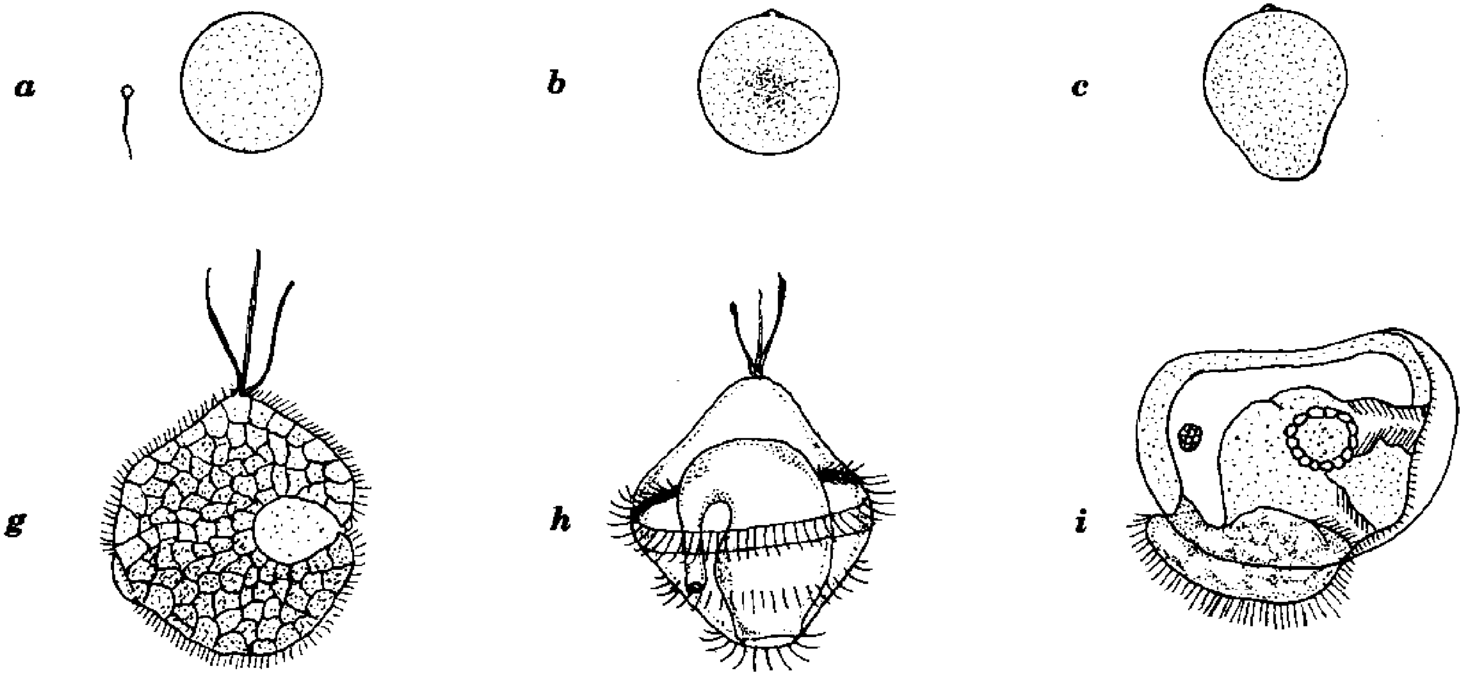
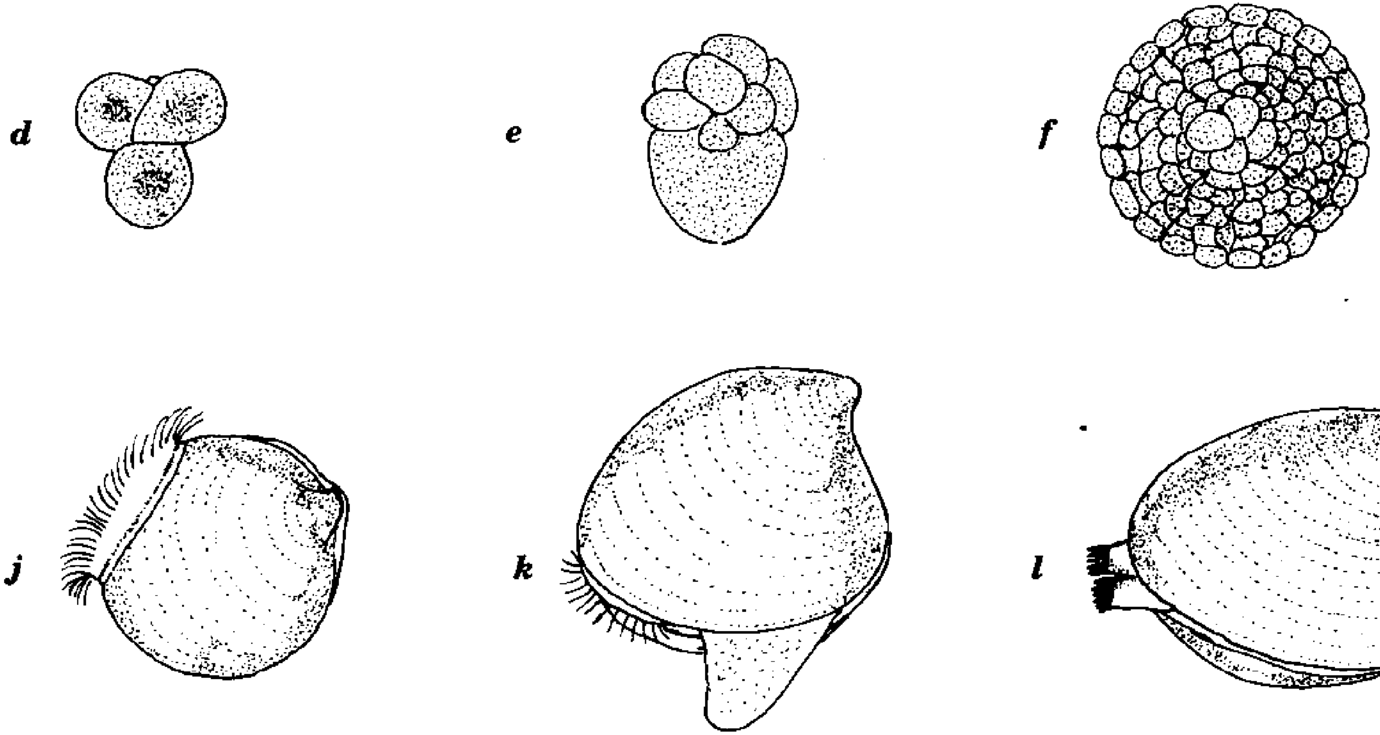


**Figure 4.** Life cycle of the quahog, *Mercenaria mercenaria*: **a)** unfertilized egg and sperm; **b)** fertilized egg and polar body formation; **c)** first cell division; **d)** four-cell embryo; **e)** eight-cell embryo showing spiral cleavage; **f)** morula; **g)** early trochophore larva (post-gastrulation); **h)** fully developed trochophore larva; **i)** D-hinge veliger larva; **j)** umbonate veliger larva; **k)** pediveliger larva; and **l)** developed post-set juvenile. Drawings by V.C. Encena.

function as it rotates like a mortar and pestle against the stiff gastric shield (23). Although quahogs do not have enzymes to digest the silica tests, or "skeletons" of diatoms, diatoms are a key food source. The anatomy of the stomach suggests that there is some mechanical crushing of the cells. There is also evidence that some ingested silt may enhance this mechanical crushing of cells (33). The stomach and associated digestive glands may also secrete some digestive enzymes (220). Much of the uptake of digested nutrients occurs in the digestive diverticula (numerous blind sacs) associated with the stomach and the intestine. A number of studies suggest that quahogs feed periodically with a rhythm that corresponds to daily fluctuations in food availability—even in continually submerged populations (22; 213). In addition to feeding on filtered particulate matter, quahogs may derive part of their nutrition from direct absorption of dissolved organic nutrients across soft-tissue surfaces (209; 252).

## Reproductive Biology and Life Cycle

Like many other bivalves, juvenile quahogs are typically males (161). In successive years they may change sex and produce eggs—a characteristic called protandric hermaphrodism. Sperm cells are much smaller than eggs and, as such, require much less metabolic energy to produce. Production of sperm cells by predominantly smaller and younger individuals allows for earlier reproductive potential among quahogs. In older, larger, and slower



growing animals, more metabolic energy can be devoted to production of sex cells, thus the switch to the larger eggs. By the time quahogs reach legally harvestable size (about 2.5 inches long), there is about a 1—1 ratio of males to females (31). In natural populations, gonads begin to produce ripe sperm and eggs during the late spring and early summer months. This corresponds to water temperature rising above 10°C (50°F) and the beginning of feeding on available phytoplankton. Once the water temperature exceeds 20°C (68°F), "ripe" adults begin to spawn (149). Quahogs do not exhibit reproductive senescence or decreased gamete production with age (31; 190; 191). A large (>90mm valve length) female may be 40 or even 50 years old and still produce 10 to 30 million viable eggs. The eggs of quahogs are 70 to 73 µm (1 µm = 1/25,400 inch) in diameter and are surrounded by a gelatinous membrane which is 50 µm thick. Both eggs and sperm of adults are expelled in the water current of the excurrent siphon; fertilization proceeds externally in the water column. The embryonic stages—which include the fertilized egg through early cell divisions, the hollow ball of cells stage or blastula, to the first larval stage (trochophore)—take from 18 to 48 hours to complete, depending on the temperature. The egg membrane often surrounds the developing embryo well into the blastula stage (153). Following the trochophore stage, successive larval stages include the straight-hinge veliger, the umbonate veliger, and the pediveliger (Fig. 4). The various veliger stages are characterized by the presence of the ciliated velum, a large sail-shaped organ

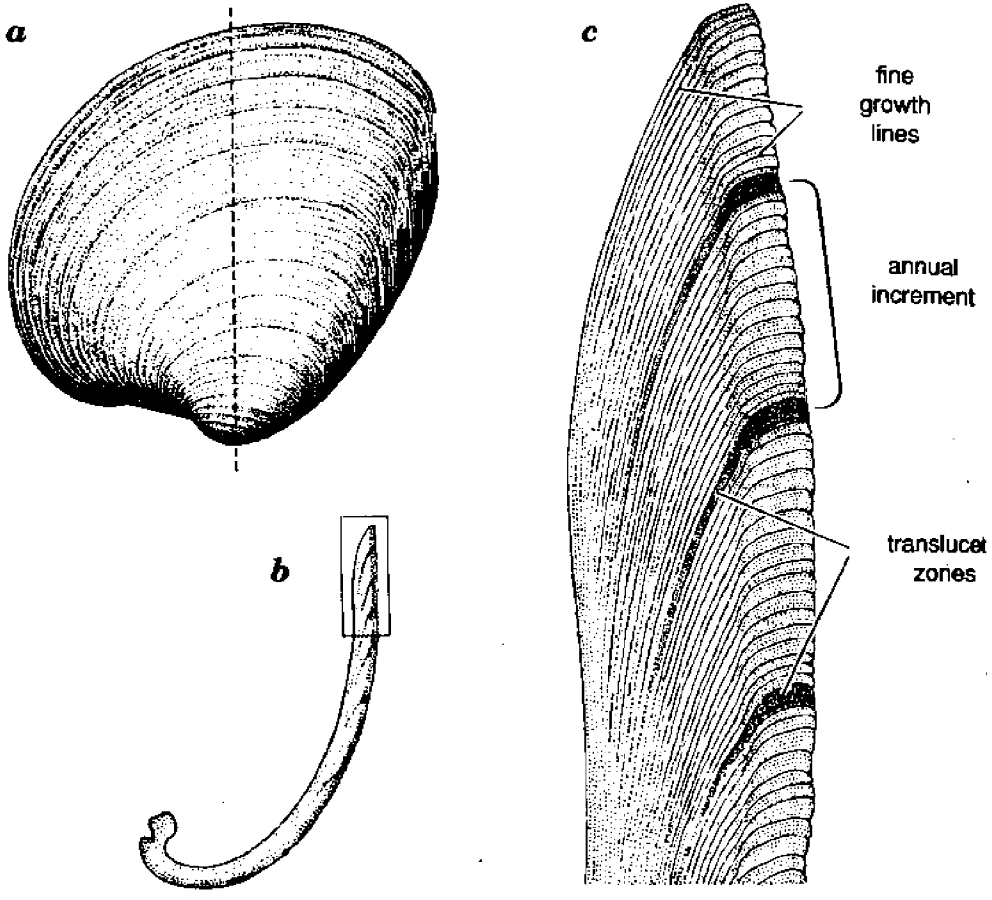


**Figure 5.** Aging quahogs using shell growth bands: **a)** yearly growth bands of *Mercenaria* can be counted by sectioning the shell from the umbo to the ventral shell margin with a lapidary saw; **b)** darker "winter break" bands are visible along the polished cut; and **c)** diagrammatic close-up of the ventral shell margin. From McManamon, F.P. and J.W. Bradley. "The Indian Neck Ossuary." *Scientific American* 258(5):98-104. Copyright 1988, Scientific American Inc. All rights reserved. Used with permission.

extending from the small larval shell that captures particulate food, generates a respiratory current, and allows for some movement of the animal in the water column. The straight-hinge veliger (also known as the "D"-hinge veliger) is given its name because of the shape of the larval shell. The larv shell of the umbonate veliger has taken on the characteristic triangular shape of quahogs, with a prominent umbo. Most of the larval stages tend t swim toward light (or opposite the force of gravity), so they tend to be conc-trated in the surface water. This is the period of dispersion by wind, waves and currents. The pediveliger stage is the final stage prior to settlement ar eventual metamorphosis to juveniles. Pediveligers are characterized by a well-developed foot that extends from the shell, and they eventually begin settle. Depending on water temperature, the time from trochophore to settlement may last from eight days to two weeks (155).

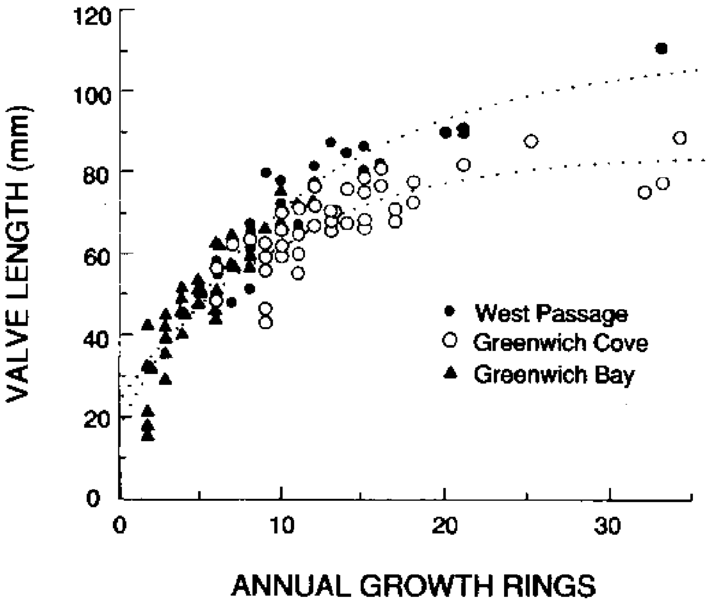


**Figure 6 (*left*).** The valve lengths of quahogs from three study sites in Narragansett Bay, R.I., are plotted as a function of estimated age. Growth curves were fit to the Greenwich Cove and West Passage data. From Rice et al. (1989). Used with permission.

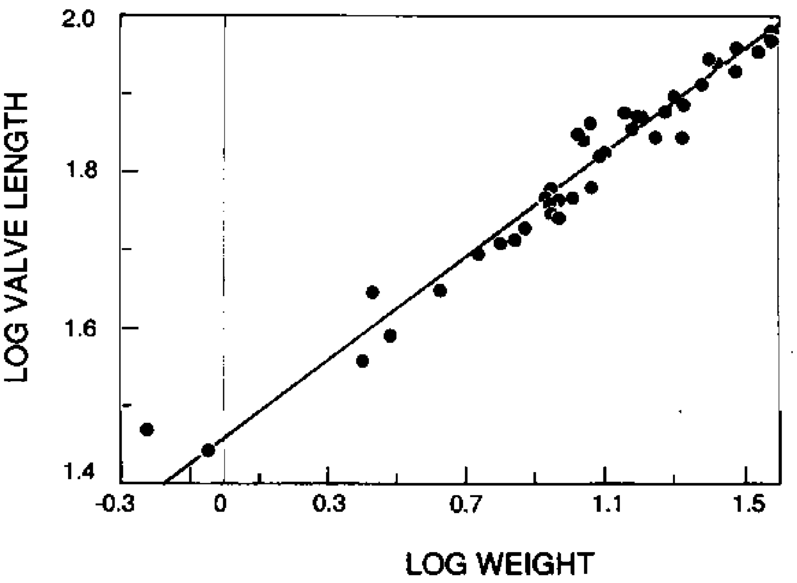


**Figure 7 (*right*).** Logarithmic plot of *Mercenaria mercenaria* valve length and weight of the soft tissues. There is a high degree of correlation (r = 0.973) between valve length and the weight of soft tissues. Data and figure from Rice et al. (1989). Used with permission.

## Growth

As previously noted, the shell grows by deposition of calcium carbonate in a network of complex organic molecules at the ventral edges. In addition, as quahogs age, there is a thickening of the shell by deposition of shell material on the inner valve surfaces. Shell growth is temperature dependent with deposition occurring mainly between the temperatures of 10°C (50°F) and 25°C (77°F), with growth ceasing below 9°C (48°F) and above 31°C (88°F) (2; 128). Most rapid growth is reported to be at 20°C (68°F) (8). In most areas within the geographical range of quahogs, the winter water temperature drops below 9°C, so growth ceases and there is an annual "winter break" recorded as a translucent layer in the shell; thus, by sectioning and polishing shells, the age of the animal can be determined (Fig. 5). In addition to the annual winter break, there are possible growth lines that correspond to slowing of growth due to excessively warm summer temperatures (98) and daily or sub-daily growth lines corresponding to periods of non-feeding and valve closure (95; 133). The growth and age of quahogs has been determined in Massachusetts (205), New Jersey (98; 133), Maryland and Virginia (90), North Carolina (196), New York (216), Georgia (243), and Rhode Island (128; 210). The rate of quahog linear growth tends to decrease with age (Fig. 6), and can be best described mathematically by von Bertalanffy's negative exponential growth equation (128). In general, the growth of soft tissues closely follows shell growth (Fig. 7), but there is a seasonality in the size and weight of somatic and gonadal tissues (117; 149; 193).

# Ecology and Environment

# 2

## Ecology

### Factors Influencing Growth of Adult Populations

The character of the bottom sediment may influence the growth of quahogs in the field (200; 201; 205). In these studies, quahogs tended to grow faster in sand as opposed to silt/clay sediments. The quantity and quality of food has an effect on bivalve growth rate (15; 80; 244; 249). In addition, other investigators have shown that increasing current speed increases the growth rate of quahogs (102; 111; 134), which has been interpreted to be a result of increased rate of food delivery to the animals. The relationship between the various factors of sediment type, current speed, and food availability is complex. It appears that excessively high current speeds can be so disruptive to normal feeding that they can inhibit quahog growth (183). A recent study was designed to determine the relative contributions of food quantity, current speed, and bottom sediment type on the growth of quahogs in the field (100). It found that the combination of food concentration and current speed (seston flux) is the major determinate of quahog growth. Sediment composition had a very minor effect on growth. Effects of sediment composition on growth, as reported in earlier studies, were reinterpreted to be a secondary effect of current speed on the distribution of sediment types. It is the higher average current speeds that usually result in both sediments with larger average grain size and in higher rates of quahog growth. A statistical model was developed that predicts quahog growth under a variety of food concentrations, current, and sediment conditions (99). The model takes into account that: a) food availability is the major determinate of quahog growth; b) sediment grain sizes are occasionally poorly correlated with current speed [e.g., New Jersey coastal lagoon (10); Narragansett Bay West Passage and

*Photograph courtesy of R.I. Division of Tourism / C. Browning*

Greenwich Bay (210)]; and c) there may be inhibitory effects of very high current speeds on growth (183).

The seston flux hypothesis implies that if the flow of seawater past quahogs is artificially increased, it is possible to increase their growth rates. There are a number of aquaculture systems that rely on this—pumping raw seawater rather than adding supplemental food (169). Food limitations can explain reduced growth rates of quahogs seeded at very high densities in aquaculture plots (49; 83; 242). It may be possible to predict stocking densities of quahogs of various sizes in a number of aquaculture applications by knowing food availability, current speed, and particle filtration rate of the quahogs at various sizes. A theoretical "carrying capacity" model has been described for mussels in suspended culture (123; 124; 158). The model relates the particle filtration rate of a population of mussels to the food available due to seston flux. The filtration of phytoplankton by quahogs has been studied (212; 245), and it is well known that filtration rate increases in relation to the weight of the soft tissues (107). From this, it can be concluded that optimal stocking densities for clams in an aquaculture plot are better estimated by using biomass or biovolume per unit area rather than simple numbers of animals. To illustrate this point, there is an unexploited population of quahogs in the Greenwich Cove portion of Narragansett Bay, R.I., with a density of 190 animals per square meter and an average valve length of 62mm (210). Individuals in the population are slow growing, characterized by "blunt" valve margins (faster-growing quahogs are called "sharps"). Suspecting that there may be density-dependent stunting or food-limited growth in this natural assemblage of quahogs, the standing crop biomass of this assemblage was compared with recommended aquaculture stocking densities. In an aquaculture application, it has been recommended that quahogs with a valve length of 20mm should not be stocked at densities exceeding 1,000 animals per square meter or reduced growth will occur (49). This stocking rate converts to 440 grams of shell-free (meat biomass) weight of quahogs per square meter. In Greenwich Cove, the shell-free biomass works out to be over 2,000 grams per square meter (conversion data in Fig. 7). Since filtration rate is a function of body weight (107), it is clear that the 190 quahogs per square meter in Greenwich Cove would be filtering three to four times as much water as the 1,000 20mm animals. Thus, it is likely that these quahogs in a dense natural assemblage are stunted due to food limitations.

## Factors Influencing Larval Settlement and Juvenile Survival

One of the factors that determines the eventual distribution of adult quahogs is the success of larval settlement and metamorphosis. Spawning of *Mercenaria* appears to be triggered by water temperatures approaching

20°C. In Rhode Island and the Great South Bay of Long Island, spawning occurs in June and July (131; 143). In the more southerly areas of the quahog range, spawning can occur in early May (82). Since the larval period of *Mercenaria* can last approximately two weeks, tidal currents and wind-generated surface waves can effectively disperse the larvae to areas many kilometers distant from the parent stock (5; 250). The dispersal of the larvae by wind, waves, and currents is facilitated by their tendency to seek light and float high in the water column. In nature, the survival of the planktonic larval stages is highly variable, but on average, only 2 percent of the early larval stages survive through to the pediveliger stage (48). As the larval stages progress and pediveligers develop, they reach a stage in which they are capable of settlement and physical change (metamorphosis), enabling them to live in the sediments. It is likely that the events of quahog settlement and metamorphosis are similar to those documented for other bivalves (59; 188). Once pediveligers become capable of settling, there are distinct changes in behavior. One of these behavior changes is a switch from light-seeking to dark-seeking behavior, causing the larvae to swim toward the bottom (6). Many of the experiments done to study the behavior of larvae at the time of settlement have not ruled out other possible larval responses. It is possible that there may be a gravity response by settling larvae (17). As the settling larvae reach the bottom, there is a substrate-seeking behavior in which the larvae touches down on the substrate and appears to crawl around (48). If a preferred substrate is not found, the larvae may return to the water column. This delay of settlement and metamorphosis can last for several days, but the selectivity for preferred substrates may decrease (188). Thus, as time proceeds, larvae may select less than optimum substrates for settlement. One study suggests that the substrate preference of quahogs is sand rather than finer silts or clays. In addition, there is a strong attraction to sediments with added "clam liquor" (quahog blood), suggesting that there may be a chemical cue (pheromone) that larvae actively seek out during settlement site selection (132). Once the larvae metamorphose, the velum, which is the key organ for larval swimming and feeding, is dropped free. The larvae become fully adapted for life on the bottom and there is no further return to the water column. This period of settlement and metamorphosis is one of the most critical in the molluskan life cycle, and a large number of larvae do not survive the transition. Preferred settlement locations appear to be important for minimizing subsequent post-settlement predation losses.

In addition to the mechanism of active substrate selection and delay of metamorphosis, near-bottom water currents have a considerable impact on the eventual location of larval settlement (75). In the case of *Mercenaria*, settlement is enhanced by the relatively low currents in seagrass beds (192).

Settlement is generally lower in open tidal channels of coastal lagoons with higher current speeds (97). The implication is that bottom currents are capable of sweeping larvae into areas of relatively low current prior to settlement. In a review of this topic, Butman (38) points out that, of the factors that have an impact on the final settlement sites of bivalves, hydrodynamic factors, such as currents, are dominant on large spatial scales from tens of meters to tens of kilometers; but on smaller scales of centimeters to meters, active habitat selection by settling larvae may be dominant. So, the currents appear to get the larvae into the proper neighborhood for settlement, but the final site choice may be by active substrate selection.

In addition to larval settlement and success of metamorphosis, post-set survival of quahogs is a critical factor determining adult distribution. Immediately after settlement and metamorphosis, quahogs lack incurrent and excurrent siphons, so they must reside on the sediment surface for a time. Turnover of sediments by deposit-feeding invertebrates may result in burial or disruption of filter-feeding, resulting in loss of the post-set juveniles (184; 206). Predation losses also account for post-settlement loss of quahog juveniles. Early work on the distribution of adult quahogs focused on the character of estuarine sediments and associated biota. Quahogs were least abundant in areas that had a high clay and silt content (200). Maximum quahog abundance was in areas of Greenwich Bay, R.I., which had moderate numbers of the tube-dwelling amphipod, *Ampelisca* (231). Very dense assemblages of *Ampelisca*—called "tape mud" by some fishermen—effectively exclude quahogs. A study in Rhode Island's Providence River showed that quahog abundances were significantly higher in areas that had sediment particles in excess of 2mm (219). Other studies, including a recent one in Florida, show similar trends of increased quahog abundance in areas with sediments containing shell fragments (97). Studies that have directly tested the survival of juvenile post-set quahogs in various substrates have concluded that large sediment grain size offers protection from predators, thus allowing for greater survival (9; 26; 50; 51; 159). Seagrass beds may also provide protection from predators (189; 192; 195).

## Quahogs as Prey

Post-set predation loss is the key determinant of eventual distribution of adult quahogs (160). One study found that lowered adult quahog populations are found in areas with abundant juvenile clam predators. Poisoning of the predators increased seven- to eight-fold the numbers of quahogs surviving to adult size (159). Recognizing that predation is of such importance to the eventual size of quahog populations, one study concluded that management approaches directed at increasing juvenile survivorship would be the most

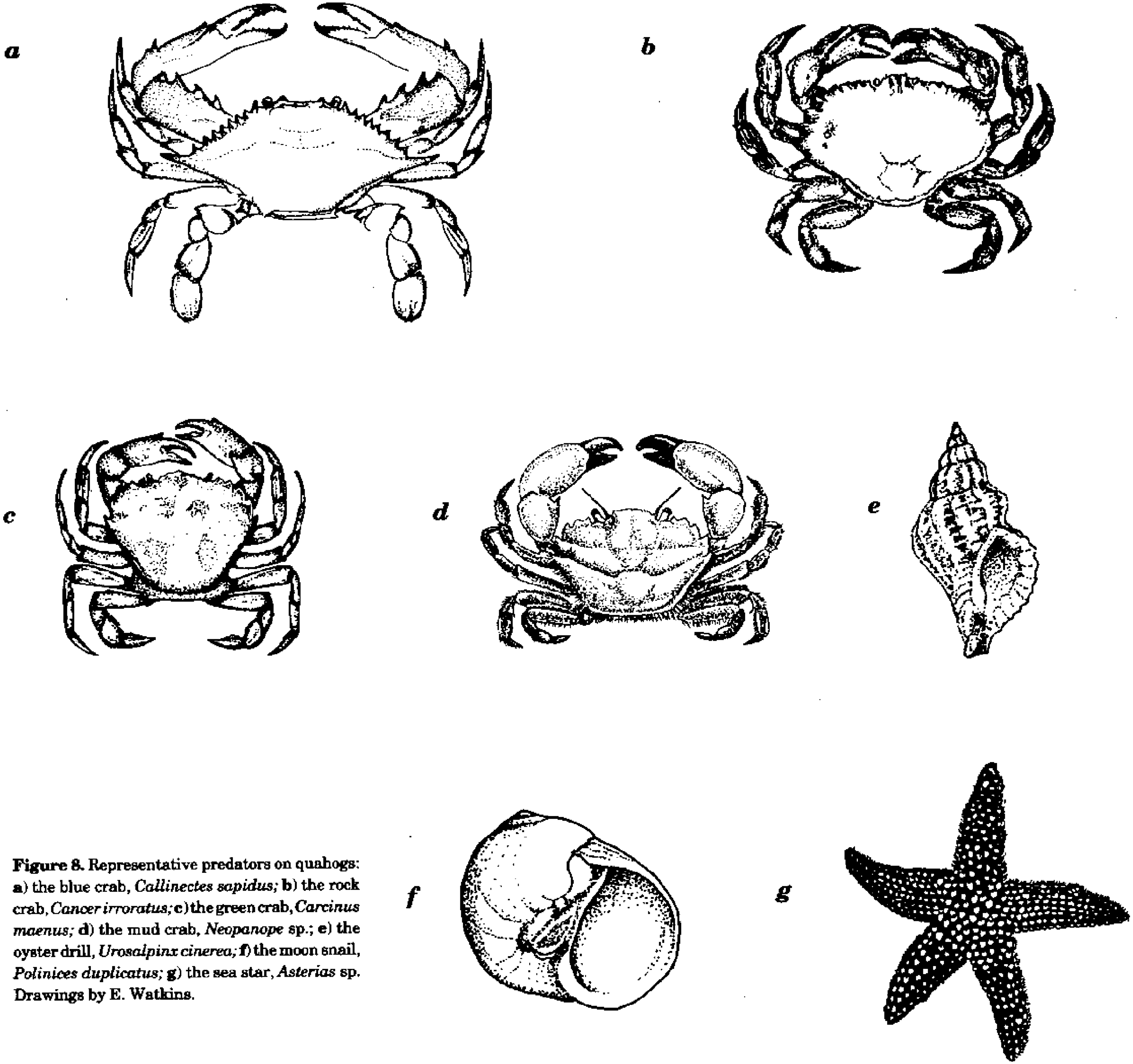


**Figure 8.** Representative predators on quahogs: **a**) the blue crab, *Callinectes sapidus;* **b**) the rock crab, *Cancer irroratus;* **c**) the green crab, *Carcinus maenus;* **d**) the mud crab, *Neopanope* sp.; **e**) the oyster drill, *Urosalpinx cinerea;* **f**) the moon snail, *Polinices duplicatus;* **g**) the sea star, *Asterias* sp. Drawings by E. Watkins.

effective in increasing productivity of quahog fisheries (164).

Aquaculturists are well aware of the necessity to protect juvenile stages from predation losses. Smaller juvenile sizes (<20mm valve length) are known to be much more susceptible to predation than larger animals (47). Successful protection of juveniles until the stage at which they are resistant to most predators can make the difference between a profitable and nonprofitable aquaculture business (49; 140).

The predators on juvenile *Mercenaria* are numerous. They include crabs such as the blue crab, *Callinectes sapidus* (Fig. 8a) (9); *Cancer* spp. crabs (Fig. 8b) (29); the green crab, *Carcinus maenus* (Fig. 8c) (246); the stone crab, *Menippe mercenaria* (170); mud crabs of the genus *Neopanope* (Fig. 8d) and related panopeid genera (144); and the horseshoe crab, *Limulus polyphemus*. Gastropod predators include whelks of the genus *Busycon* (189); the oyster drill, *Urosalpinx cinerea* (Fig. 8e); the whelk, *Thais lapillus*; and the moon snails, *Polinices duplicatus* (Fig. 8f) and *Lunatia heros*. Oyster drills and moon snails prey upon smaller quahogs by being able to bore a hole through the shell. Empty quahog shells with a single straight-sided hole the size of a pencil point are signs of oyster drill predation. Holes bored by moon snails appear to be "counter-sunk." Sea stars of the genus *Asterias* (Fig. 8g) are also known quahog predators (69; 70). Sea stars are the most important predator on adult quahogs. The large size and very thick shell make adult quahogs very resistant to most predators, but *Asterias* can effectively open them. Predatory fish include the black drum, *Pogonias cromis*, and rays, *Rhinoptera* spp., *Dasyatis* spp., and *Myliobatis* spp. (51). Other fish that are known predators on juvenile quahogs include the tautog, *Tautoga onitis*, and the winter flounder, *Pseudopleuronectes americanus*. In addition, there are a number of ducks and shore birds that prey on small quahogs. This listing of known quahog predators is certainly not exhaustive, but it does give representatives of key taxa.

## Structure of Unexploited and Exploited Quahog Populations

A number of studies have been undertaken to assess the population densities of quahogs in areas that sustain fisheries or are areas for potential fishery expansion. Walker (243) has summarized the findings of these studies. The distribution of quahogs is typically very patchy, with areas of high abundance and areas of low abundance (130; 159; 218; 219). The overall densities of quahogs in most of the areas studied typically range from 5 to 20 animals per square meter. The highest reported quahog densities in stable adult populations are 556 per square meter in the Colorado Lagoon of southern California (56), and 190 to 215 per square meter in the Greenwich Bay region of Rhode Island (210; 232). Mature populations of quahogs are charac-

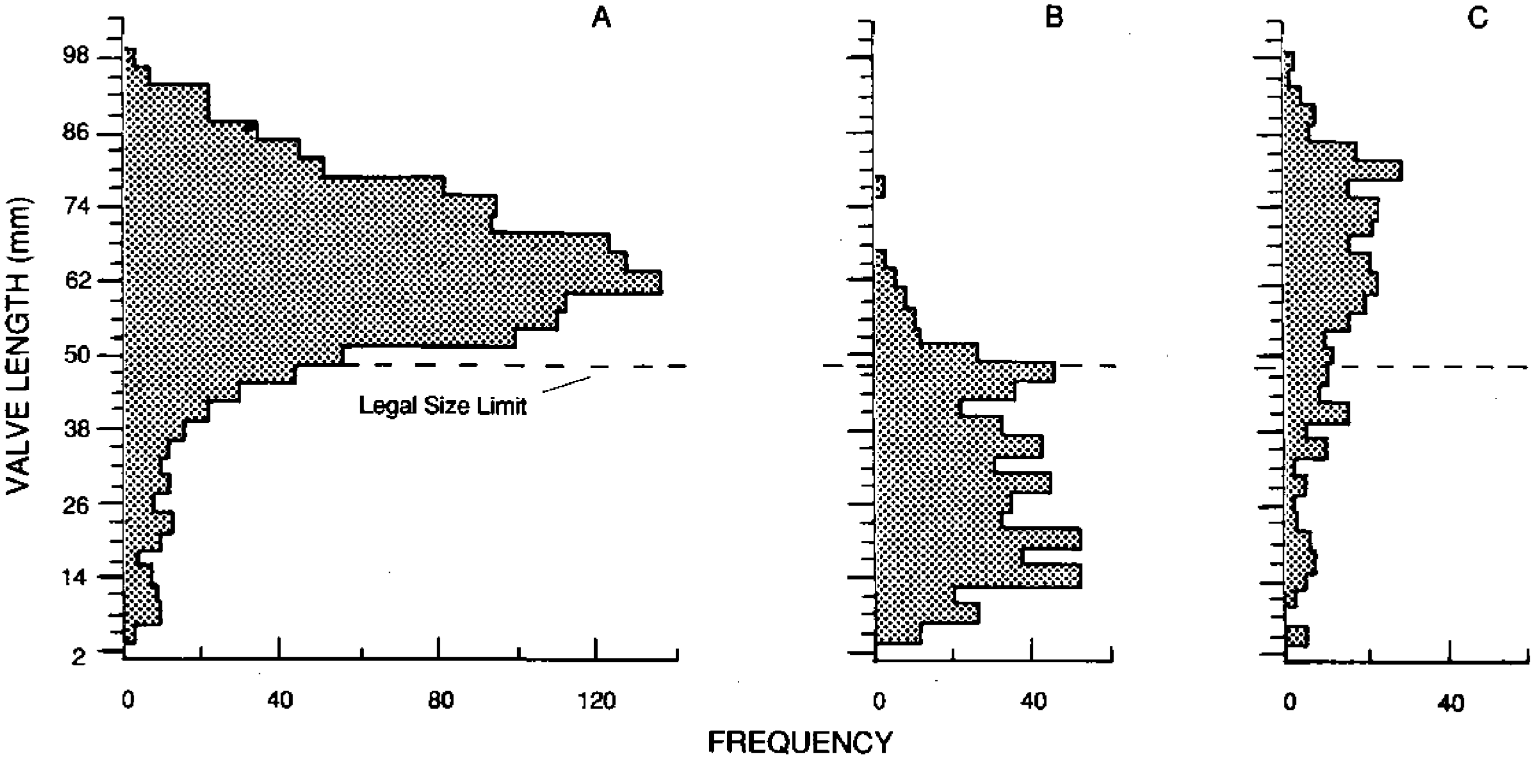


**Figure 9.** Valve length–frequency distributions of quahogs from three locations in Narragansett Bay, R.I.: **a**) Greenwich Cove, **b**) Greenwich Bay, and **c**) South Ferry. Data and figures from Rice et al. (1989). Used with permission.

terized by having a predominance of very large adults (Fig. 9a and 9c). Although recruitment in some areas may be sporadic, or recruitment rates may be very low, mature populations have size-frequency distributions (such as those in Fig. 9a and 9c) that are uniform with a single peak and with relatively few juvenile quahogs present (162; 243). It appears that large populations of mature quahogs can effectively exclude recruitment of younger individuals. This exclusion of recruitment into areas with large adult populations has also been found to occur in dense assemblages of the European cockle *Cardium edule* (109). Explanations for the lack of recruitment into large assemblages of adults include the following: starvation of post-set juveniles due to intense competition for food; greater losses from predation among post-set juveniles due to slowed growth because of food limitations; an external cue from adults preventing settlement; or direct filtration of larvae from the water column by the adults (175). A more recent study suggests that the mass water flow of water plumes from excurrent siphons of bivalves in dense assemblages may effectively prevent larval settlement (37). In heavily fished areas, large quahogs are effectively cropped from the population (Fig. 9b), and younger animals dominate (243). With the removal of the adults, there is an increase in the absolute number of smaller animals, perhaps resulting from the removal of competition for space and food by the adults. Other explanations for this enhancement of smaller size classes in areas with few adults is that back eddies forming at the base of excurrent siphonal plumes of solitary adult quahogs in scattered distributions may actually enhance the settlement of larvae (81), or that in some way, the action of fishing may modify the physical environment (sediments) in such a way that post-set predation is minimized.

### Quahog Assemblages as Modifiers of the Environment

Since bivalves such as *Mercenaria* are active filter feeders, and dense assemblages can potentially filter a large quantity of particulate matter from the overlying water column, a number of authors have postulated that dense assemblages of filter-feeding bivalves can act as a major intermediary in nutrient transfer between the water column and sediment environments (61; 135; 142). In this respect, one study suggests that filter-feeding bivalves can control the overloading of estuaries with excess organic material (eutrophication) by filtering out excess phytoplankton stimulated by nutrient loading (186). Thus, the quahog beds can, in some cases, act as a natural pollution control. As an example of this phenomenon, communities of estuarine mussels were found to effectively clear the waters of a small Massachusetts estuary of phytoplankton, with one bivalve species (*Geukensia demissa*) being very effective at filtering bacteria-sized plankton (251). Other studies carried out in mesocosms—large seawater tanks simulating Narragansett Bay—examined the rates of particulate carbon deposition (sedimentation) by quahog assemblages, as well as the rates of nutrient release by the sediments (71; 72; 73). The results of these studies showed that quahogs were able to increase the rate of transfer of particulate material from the water to the sediments through their filtering activity. In addition, the increase in organic material delivered to the sediments stimulated greater release of nutrients (natural fertilizers) from the sediments. This release of extra nutrients from the sediments to the water column in turn further stimulated phytoplankton production. The overall productivity (amount of total biomass production) was higher in the mesocosms containing quahogs. In brief, the quahogs were able to stimulate processes in the entire ecosystem by providing an important link between the sediments and the overlying water.

## Effects of Environmental Factors

### Effects of Temperature

Larvae of quahogs have been successfully grown through to metamorphosis between the temperatures of 18°C (64°F) and 30°C (86°F) (156). Above

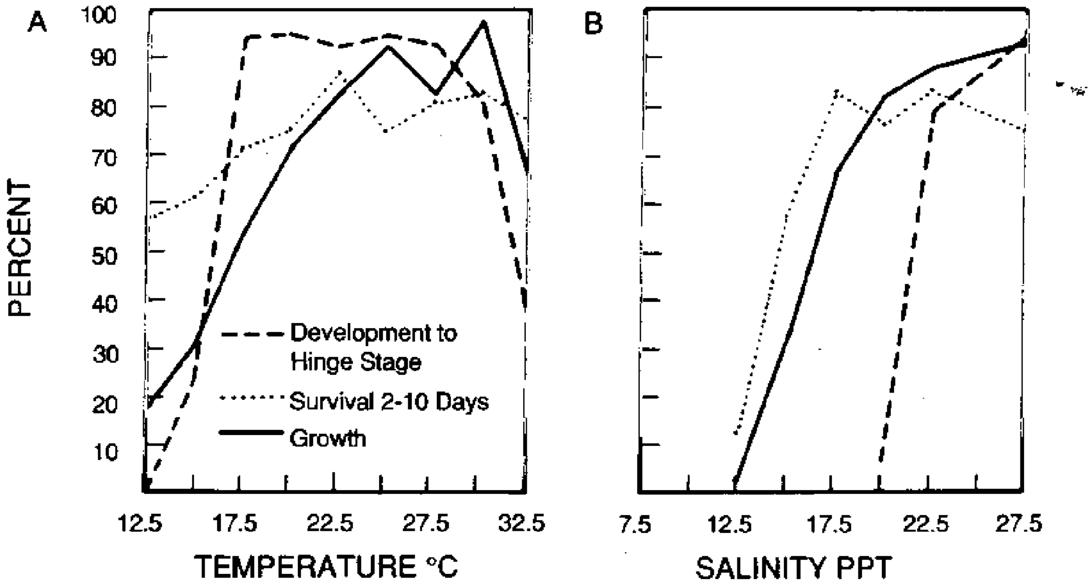


**Figure 10.** Growth of quahogs at different temperatures (A) and salinities (B). Redrawn from Davis (1969).

33°C (91.4°F) and below 15°C (59°F), larvae do not develop properly and there is high mortality (Fig. 10a). Temperature also affects the rates of shell opening and growth of adults (151; 239). Overall metabolic rate increases with increasing temperature (237). Activity ceases at temperatures below 10°C (50°F) and above 31°C (88°F) (2). (See previous section on growth.)

## Effects of Salinity

Salinity refers to the relative salt content in waters and is typically measured in parts per thousand (ppt); that is, grams of salts per kilogram of pure water. Typically, fresh water will have a salinity of 0 ppt and seawater will be 34 to 35 ppt. In a few instances, natural waters may have salinities higher than seawater, such as desert salt lakes and some coastal embayments in very arid regions. Estuaries—bodies of water in which fresh and seawater join and mix—are the habitat for quahogs. These range in salinity between the fresh water and seawater extremes. Quahog embryos develop optimally at a salinity of 27.5 ppt. Early-stage larvae cannot develop in salinities below 17.5 ppt. The upper salinity limit for *Mercenaria* larvae is 35 ppt, but only few larvae can develop normally at this salinity. Veliger larvae can survive and grow in 17.5 ppt salinity, but below 15 ppt settlement and metamorphosis is inhibited (62) (Fig. 10b).

Adult quahog densities are generally highest in estuarine waters between salinities of 18 ppt and 32 ppt. There is some evidence that metabolic rates of quahogs are higher in lower salinity waters (237). Within the estuarine environment, organisms can be exposed to periodic salinity fluctuations that may exceed the normal physiological tolerance limits. One response of the quahog to these periodic salinity shifts may be simple valve closure, which would effectively prevent exposure to the transient salinity extreme (222; 223). Quahogs can maintain valve closure for several days by respiring anaerobically. If altered salinity regimes are prolonged, quahogs have the capacity for some physiological adjustment to the altered osmotic conditions. The various salts and other small molecules dissolved in the cells have the tendency to draw water. As seawater salinities drop, more water is drawn into the cells because of the relative differences in dissolved materials, and the cells begin to swell. In very low salinities, the cell swelling can be so severe that cells burst and the quahog is killed. Intracellular volume regulation is carried out by adjusting the amount of osmotically active solutes (mostly free amino acids, which are simple organic molecules that can be used as the building blocks for proteins) in the cells. In adapting to lower salinity, free amino acids are released by quahogs to the external environment, so that water follows by diffusion and the cells shrink to their original size (209). Another mechanism for intracellular volume regulation by quahogs may be increased metabolic oxidation of the free amino acids and increased excretion of ammonia (14; 113). In conditions of increasing salinities, the opposite problem occurs. The cells tend to shrink because water is drawn out of the cells into the more concentrated salts in the seawater. Adaptation to increased salinities may involve use of amino acids derived from protein in the diet, or biosynthesis of these small molecules from metabolic precursors (25), or by uptake of the amino acids from the external environment (209).

## Effects of Oxygen

Most marine organisms require oxygen to carry on metabolic activity. Oxygen in natural waters is typically produced by photosynthesizing plankton or other aquatic plants, or diffuses into water from the atmosphere. Typically, well-oxygenated seawater will be in excess of 5 milligrams oxygen per liter (mg $O_2$/L). Low oxygen conditions (hypoxia) can occur in estuaries as a result of eutrophication and the decomposition of organic wastes. Embryonic and larval quahogs appear sensitive to low levels of dissolved oxygen in the water column (182), with all individuals dying if held in 0.2 mg $O_2$/L. Larvae can survive at levels above 0.5 mg $O_2$/L. Optimum growth occurs when oxygen concentrations are above 4.2 mg $O_2$/L. Growth is severely impaired at dissolved oxygen concentrations below 2.4 mg $O_2$/L.

Whether by valve closure for protection from salinity extremes, pollutants, or low oxygen in the water, adult bivalves such as *Mercenaria* are known to have a high capacity for being able to carry on metabolic activity in the presence of greatly reduced or zero levels of oxygen (anaerobic metabolism) (66; 67; 106; 107). In *Mercenaria*, lactic and succinic acids are produced as products of anaerobic metabolism (58; 103). The production of these organic acids during anaerobic metabolism leads to lowered pH in the mantle cavity. The pH shift is buffered by the quahog through dissolution of the shell, which releases calcium carbonate (58; 74). For this reason, quahogs are known to have thin or eroded shells when collected from areas that are prone to low oxygen (hypoxia). Periodic valve closures corresponding to daily cycles of inactivity have also been shown to result in shell dissolution, visible in the shell as microscopic daily or sub-daily bands (95). There is evidence that under conditions of very low oxygen, different tissues, such as muscle and mantle tissue, can utilize entirely different biochemical reactions for generating energy through anaerobic metabolism (139). These additional biochemical pathways exist in quahogs to allow anaerobic metabolism to occur without producing acidic end products. These are very important biochemical pathways in that they allow much longer-term metabolism in reduced oxygen without the pH balance problems. Enzymes that direct these metabolic reactions (alanopine and strombine dehydrogenases) have been isolated from gill and foot muscle tissues of *Mercenaria* (87). There is evidence that even in adequately high oxygen concentrations, the various anaerobic biochemical systems of *Mercenaria* are actively producing metabolic energy (104). The process of filter feeding by quahogs is closely associated with oxygen uptake. It has been suggested that oxygen demand by *Mercenaria* may be the controlling factor determining the rate of water pumping by the gills (108), but this remains controversial (238).

## Effects of Pollutants

Bivalve mollusks, including *Mercenaria*, have been used extensively as research models for pollution studies (60). Bivalves possess a number of characteristics that make them attractive as pollution indicators and research models. First, they inhabit estuarine and coastal marine areas, which are prone to pollution. Second, they are sessile, so they cannot migrate away from the pollution source. Third, bivalves generally live for a long time, making long-term studies feasible. Fourth, broad geographic distribution of some species aids in the comparison of widely separated geographic areas. Fifth, the physiology and ecology of commercially important species are well-studied, providing valuable baseline information. Finally, many species of bivalves are easily collected and therefore readily available to researchers.

It is known that various heavy metals, such as copper, lead, mercury, cadmium, and zinc in the water column, are much more toxic to embryonic and larval quahogs than to the adults (42). Concentrations of heavy metals at sublethal concentrations cause slowed larval growth and development. In addition to metals, there is evidence that pesticide residues and petroleum-derived hydrocarbons may be very toxic to quahog larvae (39; 63; 122). Losses of larvae through acute toxic effects or by sublethal decreases in fitness of larvae (leading to predation or disease losses) are possible reasons for reduced recruitment into benthic populations (41).

A number of studies document the concentration of heavy metals in adult quahog soft tissues and the rates of accumulation and release (depuration) under varying environmental conditions. It has been generally shown that quahogs can accumulate metals from seawater, but are slow to release them when placed in cleaner water (19; 88; 146; 215). Heavy metal concentrations found in quahog tissues tend to be highly variable, depending on salinity, temperature, season, age, and the degree to which the gonads are developed. (18; 215). Some studies have focused on uptake of metals by quahogs in contaminated sediments. These studies have yielded conflicting results, with some studies (19; 236) showing transfer of metals from sediments to quahog soft tissue, and another (217) showing no transfer of metals from contaminated sediments during 100 days of exposure. It is highly likely that these conflicting results can be explained by differing sediment chemistry characteristics between the sites. Rates of metal release or mobilization and bioavailability of the metals may be quite different in different sediment types (121).

There are three general physiological effects of metal poisoning in marine organisms. First, functions of various enzymes (proteins that catalyze biochemical reactions) may be affected. For example, replacement of metals in metalloenzymes may severely impair their function (54; 214). Also, the function of sulfur-containing (sulfhydryl) enzymes may be similarly impaired (227). One mechanism to counter the toxic effects of metals on proteins is for the animal to synthesize replacement proteins. The chronic demand for protein turnover is costly in terms of metabolic energy and can interfere with growth (199; 207). Second, enzymes and/or binding proteins (such as metallothioneins) are induced to provide a means for detoxification of the metals (46; 137). These metal-binding proteins have a high capacity for scavenging metals and act to protect other proteins from damage by the metals. Finally, damage to external tissue layers (epithelia), or gill cilia in the case of bivalves, may interfere with respiratory and feeding mechanisms (145; 214).

A number of studies have been undertaken to assess the toxicities, uptake, and depuration of various hydrocarbons associated with petroleum products (3). Of the various hydrocarbons associated with petroleum, the polycyclic aromatic hydrocarbons (PAHs) and lighter volatile straight-chain (aliphatic) hydrocarbons appear to be the most toxic to bivalves (180; 211). Bivalves accumulate hydrocarbons from both particulate and dissolved forms in the water column, and it has been reported that some classes of hydrocarbons, especially shorter-chain hydrocarbons, are rapidly released once the animal has been placed in clean seawater (147). Studies with *Mercenaria* have shown that a number of petroleum-derived hydrocarbons can be accumulated from the environment (28; 86). Many of these accumulated hydrocarbons, especially longer-chain and cyclic hydrocarbons, are very persistent in soft tissues (28). Petroleum hydrocarbons and other pollutants are known to impair the immunological disease-fighting capability of quahogs (4), as well as cause pathologic lesions (233).

# 3

# Fisheries

The quahog fishery is one of the largest along the Atlantic coast of the United States. According to the National Marine Fisheries Service statistics for 1987, 11.4 million pounds of quahogs were landed, with a dockside value (money paid to the fishermen) of about $49.6 million. The value of all fisheries along the Atlantic coast (excluding the Gulf of Mexico) in 1987 was $847.8 million, with quahogs making up 5.9 percent of the total value. The only Atlantic coast fisheries surpassing the quahog fishery in value were the lobster fishery with 12.7 percent, and the blue crab fishery with 8.3 percent of the total value. The increasing demand for quahogs by the public is reflected in the general trend of its increasing dockside value (Fig. 11). The overall quantity of quahog meats landed on an annual basis has been highly variable, and there is no general long-term trend of increased harvests since the 1960s. It is likely that natural stocks are now being exploited at rates that are likely to be close to the maximum allowable without depleting the stocks—called the maximum sustainable yield (MSY) (172; 173).

As previously noted, quahogs have been harvested in New England since pre-colonial times. By the turn of the 20th century, the fishery in New England was well developed, and state governments were considering measures to manage the stocks (20). Presently, commercial and recreational quahog fisheries are significant in all Atlantic coastal states from Massachusetts to Florida.

## Fishing Methods and Gear

It is generally accepted that the earliest method of harvesting quahogs consisted of hand collection, or use of simple harvesting tools, such as shovels and rakes, along the shore between the high and low tide marks (intertidal

*Photograph from the Rhode Island Historical Society*

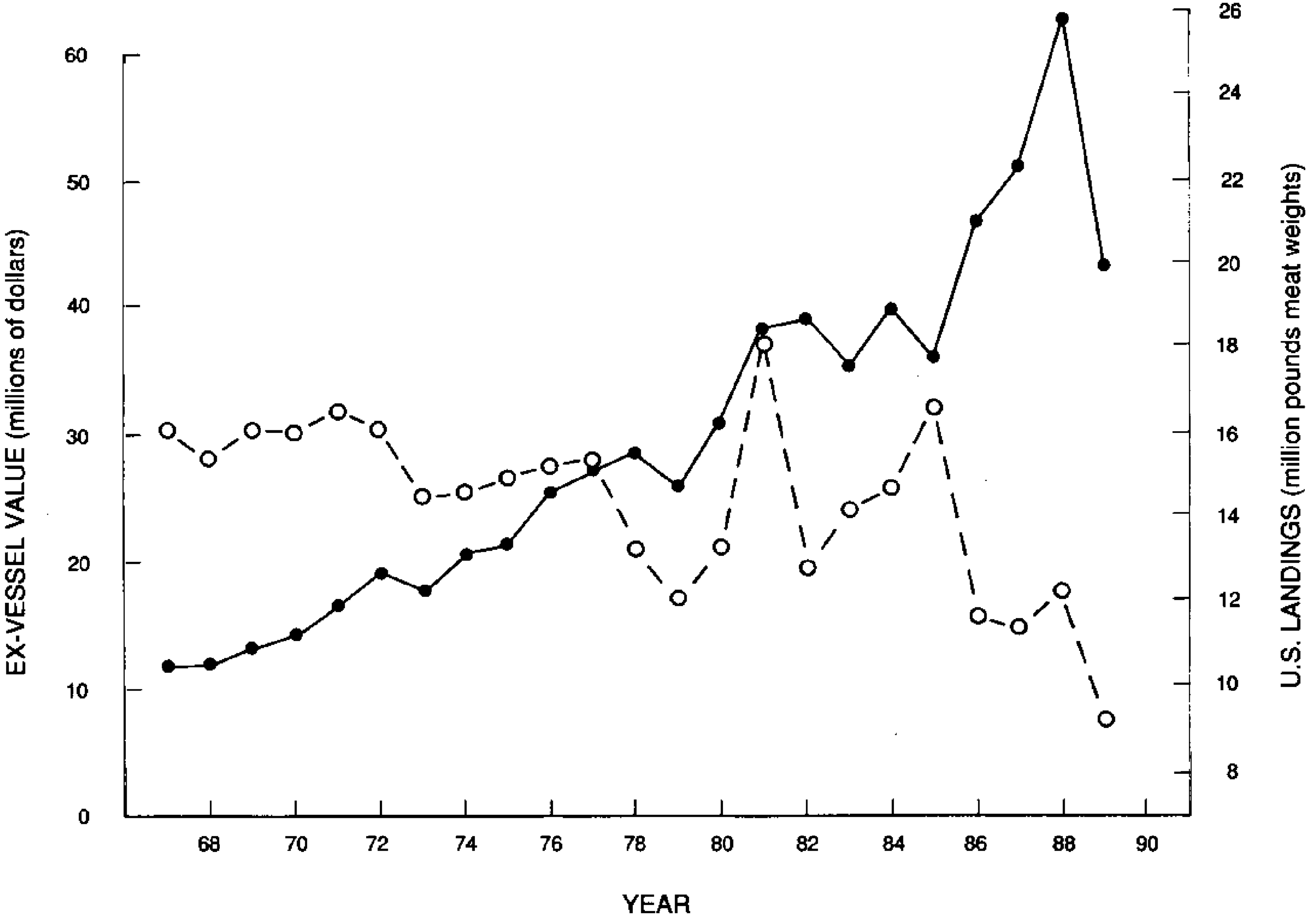


**Figure 11.** Landings of quahogs 1967 to 1989. Open circles represent landings in shucked meat weights and closed circles represent the value in millions of dollars. Data from NMFS statistics.

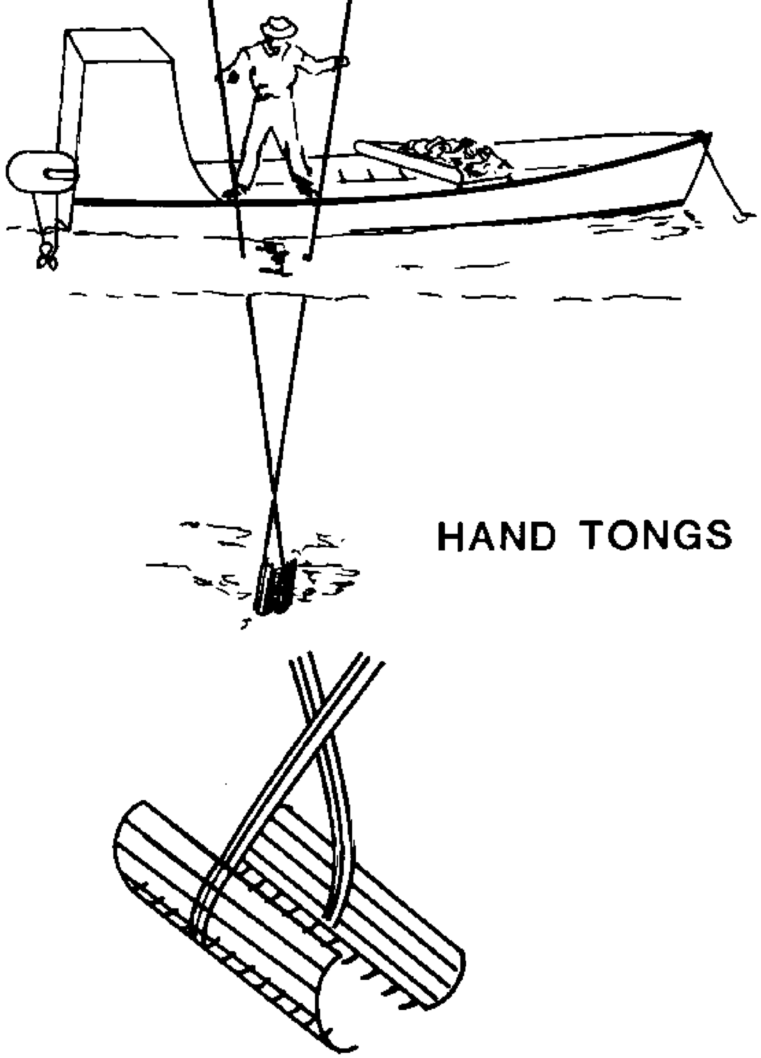
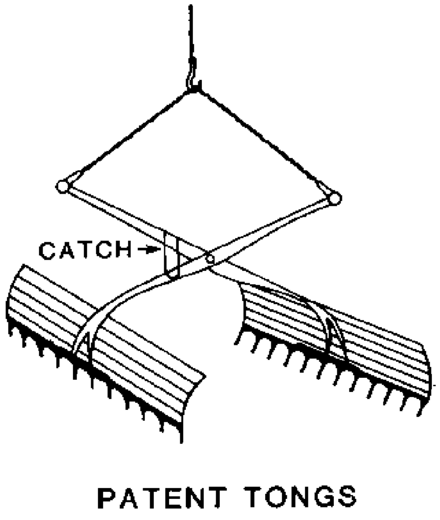
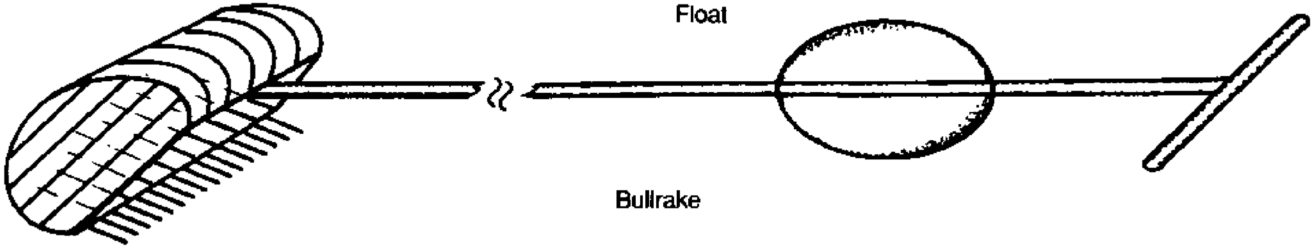


**Figure 12** ***(right).*** Hand tongs for harvest of quahogs in shallow sub-tidal water. Drawing by E. Watkins.

**Figure 13** ***(below).*** Patent tongs allow for harvest in waters deeper than 15 feet.



zone). Since the late 1800s, tongs have been used to harvest quahogs from waters beyond the intertidal zone (Fig. 12). Due to the scissors action of the handles of the tongs and the physical limit as to how wide the tong handles could be opened by the arm spans of the fishermen, they are limited to working depths of about 12 to 15 feet of water (30). Although tongs are limited in working depth, they are the gear of choice by some "traditionalists" who claim that tongs are the most efficient hand-operated tool for shallower waters. The patent tongs (Fig. 13) offer a means for fishing in deeper waters (76). The patent tongs are tethered and dropped from a boat. A catch mechanism allows for closure of the tongs as they hit bottom, and then they are retrieved by the tether rope. Patent tongs are now very rarely seen in the quahog fishery, because most fishermen prefer bullrakes for harvesting quahogs in deeper waters.



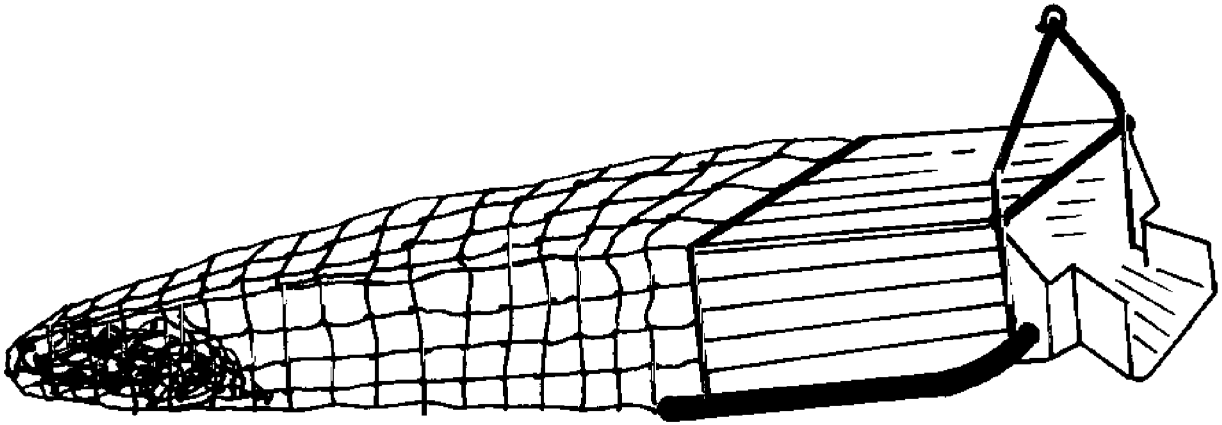


**Figure 14.** The bullrake is the most popular of the hand-operated fishing implements in the quahog fishery of the Northeast. Typically, the stales (handles) are 50 feet or longer and allow harvest in 25 feet of water. The float near the "T-bar" handle allows the stale to float as the rake head is retrieved from the bottom.

**Figure 15.** Mechanical dredges, such as the rocking chair dredge, are very efficient for harvesting quahogs, but their use is restricted in many states because their efficiency is often responsible for overexploitation of stocks. Drawing by E. Watkins.

The hand-operated harvesting device most widely used for quahog fishing is the bullrake (Fig. 14). The bullrake is said to have been invented in the late 1940s by a shellfisherman from Long Island, N.Y. (30). In the mid-1950s, the bullrake was adopted by a few fishermen in the Greenwich Bay region of Rhode Island. By the late 1960s, bullrakes had become the industry standard in all of New England, New York, and south to the southern Atlantic states (194).

The bullrake head has evenly spaced teeth to extract quahogs from the sediment and an integral basket to hold the quahogs as they are hauled to the surface. The earliest bullrakes had wooden stales (handles) that were often 30- to 40-feet long, which allowed fishing in about 20 feet of water. Individual sections of the old wooden stales were held together by iron rings. As a general rule, a bullrake can harvest in waters roughly half as deep as the length of the stale because the optimum leverage is reached when the rake is at an angle, not perpendicular to the estuary bottom. Introduction of aluminum stales in the 1960s allowed for longer poles and harvesting in about 30 feet of water. Currently used bullrakes have specially designed heads for varying bottom type. A variant of the standard bullrake is the "short-stick" bullrake (also known as the "donkey rake" in some localities), which has a greatly shortened stale for harvesting quahogs in shallow water by a wading fisherman. Aluminum stales are currently the most popular, but up-to-date fiberglass and graphite composite materials have been used by some to make stales stronger, lighter, and longer. Some fishermen working Rhode Island's Narragansett Bay are known to fish with 90 feet of stale, allowing them to harvest in excess of 45 feet of water.

The use of diving equipment in the quahog fishery has allowed for exploitation of waters that are inaccessible to implements such as tongs and rakes. Typically, a metal diving basket will be tethered to the diver's boat. The diver will then fill the basket with quahogs and a tender may haul the basket aboard. Another alternative used by divers is to fill mesh bags with quahogs and to tie them to buoyed lines. After the day of fishing is completed, the buoyed line with the attached quahog bags is retrieved. The direct collection of quahogs from the sediments is usually by use of simple hand tools. A number of fishermen will use an air line attached to a small compressor aboard their boat. The compressed air is used to blow off a top layer of sediment to expose the quahogs, after which they are collected by hand. Some divers will work in the winter months by using dry suits to protect themselves from the cold water.

Mechanical harvesting gear has been used in some areas as an effective means for harvesting quahogs. One method, called "clam kicking," is practiced in North Carolina (197). The clam kicking technique is used in shallow estuarine sandy-bottom areas or seagrass beds and involves the use of a boat with an outboard motor. The outboard motor is used to stir up sediments and dislodge quahogs. The quahogs are then simply raked up from the disturbed sediments and brought aboard the boat. Other quahog harvesting methods include mechanical and hydraulic dredges (218). A mechanical dredge, such as the "rocking chair" dredge (Fig. 15), is pulled along the bottom and is designed to dig into the sediments with an up-and-down motion. As the dredge proceeds, quahogs are kicked into a trailing chain bag. Hydraulic dredges are similar to the mechanical dredges, but work more efficiently. The hydraulic dredges work by having a water pump on board a boat that is connected by a hose to multiple water jet nozzles (manifold) on the dredge. Water sprayed from the manifold acts to liquify the sediments as the dredge passes so that the quahogs can be quite efficiently picked up and passed to the trailing chain bag. Mechanical and hydraulic dredges have been used in some states for harvesting quahogs (30), but have now been banned because they are too efficient, possibly posing a threat to the sustainability of the fishery.

### Fishery Management Regulations

In most instances, fishery management regulations are designed to prevent overexploitation of the quahog resource (see previous discussion of population structure of exploited and unexploited quahog populations). Authority for management of quahog fisheries varies from state to state. In some states, the management of the fishery falls under the jurisdiction of state officials; but in other states, shellfishery management is largely under the control of local municipalities.

A number of regulations are designed to limit the fishing effort in a given area. These regulations include:

- **a)** Restrictions on gear type
- **b)** Limitations on time of day for harvesting
- **c)** Seasonal limitations on harvesting
- **d)** Daily catch limits
- **e)** Licensing requirements and limited entry to the fishery

Other regulations are designed to protect the adult quahog brood stock. These regulations include:

- **a)** Minimum sizes for harvest (1-inch hinge width in most states of the Northeast)
- **b)** Regulations on bar spacings in harvest gear (teeth spacing on rakes and tongs, mesh sizes on dredge bags, bar spacing on diver's baskets)
- **c)** Maintenance of closed areas as “spawner sanctuaries” (171)

### Water Quality and the Fisheries

Since quahogs are sedentary filter feeders, there is concern that they will potentially accumulate pollutants or pathogens (disease-causing organisms) from the water, potentially posing a health threat to the public (44). For example, varying amounts of petroleum hydrocarbons can be passed on to the public if quahogs are harvested in polluted waters (202). Current efforts by the U.S. Environmental Protection Agency have focused on developing models to predict public health risk from the consumption of seafood contaminated with various metallic and hydrocarbon contaminants (136).

Shellfish accumulating pathogenic microorganisms associated with sewage have been a major threat to public health. In response to repeated outbreaks of typhoid fever and cholera associated with bivalves, the National Shellfish Sanitation Program (NSSP) was established in 1925 to set natio wide water quality and post-harvest handling procedures to safeguard public health. The NSSP was incorporated into the Interstate Shellfish Sanitatio Conference (ISSC), a group of public health officials from various shellfish-producing states and officials from the U.S. Food and Drug Administration For states to engage in interstate commerce of bivalve shellfish, including *Mercenaria mercenaria*, they must comply with the various sanitation provisions of the ISSC (125; 126). Sanitation regulations include microbiological standards for shellfish-producing waters, microbiological standards for shellfish meats at harvest, proper handling of shellfish at harvest, and proper handling of shellfish as they pass through the marketing channels.

In most instances, quahogs are harvested from waters that are certifie as clean by state agencies under ISSC guidelines. The ISSC guidelines do, however, allow for harvest of shellfish from moderately polluted waters, provided that some form of post-harvest disinfection is undertaken. The mo common forms of post-harvest disinfection are transplant, relay, and depuration. Transplant involves the harvest of juveniles from seed beds th may be in polluted waters, and transferring them to certified clean waters f final grow out to adult size. A key feature of transplant is that the final gro out may take several months to years. Under ISSC guidelines, transplant stock can originate in moderately to heavily polluted waters, because very long cleansing periods in certified clean waters are involved. Relay differs from transplant in that quahogs of legally harvestable size are harvested from lightly polluted waters and transferred to certified clean waters for periods of time ranging from a few weeks to a few months. Because of the shorter time periods for cleansing, quality standards for source waters of relay shellfish are stricter than the transplant standards. Relay may involv the replanting of quahogs into the sediments of certified waters (93), or the holding of quahogs in bags or enclosures off-bottom (240). In depuration, quahogs are held in shore-based tanks supplied with clean seawater (92). The rates of elimination of bacterial indicators by the quahog are affected b various environmental and seasonal factors (40; 114). As a result, usually 4 to 72 hours depuration time is allowed in sufficiently warm and oxygenated water for reductions of bacterial indicators in shellfish meats to occur.

There is evidence that viruses may take considerably longer than the standard two to three day depuration period to be eliminated by quahogs. Coliphages—viruses that attack bacteria—are commonly found in sewage. They are not harmful to humans, but they are retained in the digestive trac of quahogs very much like viruses that can cause human disease. The coliph age S-13 virus can take weeks to be fully eliminated under optimum conditions (43). Recent work with the MS-2 coliphage indicates that depuration of this virus from *Mercenaria* may take several weeks to months (36). These results suggest that in the interests of public health, special care must be taken to assure sanitary quality of harvesting areas. Depuration can add an extra margin of safety to bivalve shellfish, but it is not a substitute for environmental pollution abatement.

Toxins associated with some species of phytoplankton are a potential health threat to the shellfish-consuming public. This is because filter-feeding allows for accumulation of toxins in bivalve soft tissues. Shumway (224) provides a recent review of the impacts of toxic algal blooms on shellfisheries and aquaculture. The dinoflagellate, *Alexandrium fundyense* (formerly *Protogonyaulax tamarensis*), responsible for "red tides," produces the toxin responsible for paralytic shellfish poisoning (PSP). During one major red tide event in Massachusetts, various species of bivalves were shown to be very toxic, including mussels, *Mytilus edulis*; soft-shelled clams, *Mya arenaria*; and scallops, *Argopecten irradians*, but quahogs remained completely free of the toxins. Laboratory studies have shown that quahogs will retract their siphons and completely close their shells if there are bloom concentrations of *Alexandrium fundyense* in the water (225). However, another laboratory study suggests that quahogs can accumulate algal toxins if dinoflagellates are in mixtures with other phytoplankton, as is likely in the natural aquatic environment (34). Quahogs might accumulate some of the toxins if there is a red tide event; however, they will tend to release the toxins in a few days (34). The exact conditions for the initiation of an *Alexandrium* bloom are not well understood, but they are much more common during the warm summer months. States such as Maine, with major shellfish industries, have programs to closely monitor the appearance of red tides (226). Toxins associated with the phytoplankton *Dinophysis* are responsible for diarrhetic shellfish poisoning (DSP). DSP is manifested as mild to moderate gastroenteritis, and there have been no known fatalities. Quahogs can accumulate the DSP toxin. Like PSP, the incidence of DSP is higher during the warm-water summer months (89).

## Economics of the Fishery

Key economic aspects of the quahog fishery include sustainability of yields and market demand considerations. Holmsen (118) provides an excellent analysis of the various factors influencing the Rhode Island quahog fishery, which consists mainly of bullraking by individuals in small boats. Since the 1960s, the landings of quahogs have been variable, but there has been no general increasing or decreasing trend in catches (Fig. 11). One key aspect of the industry is that during poor economic times in other sectors, the number of shellfishermen increases, thereby increasing fishing effort (119). An economic analysis by Gates (94) suggests that increasing demand for bivalve shellfish, including quahogs, coupled with a fairly constant fishery supply has resulted in increasing prices. Increasing demand for the product has spurred increased imports of clam meats from abroad. It has been suggested that fishermens' cooperatives can provide for greater stabilization of market prices and stabilization of fishermens' incomes. This is due to the power of cooperatives to limit the supply of perishable product entering the market at a given time, and the ability of cooperatives to encourage innovation and more efficient methods of harvest (94).

# Aquaculture

# 4

Increasing market demand for quahogs has provided the impetus for greater interest in quahogs as an aquaculture species. The feasibility of aquacultural production of quahogs has been discussed from the 1930s (150), and the methods for artificial propagation of quahogs have been developed at the National Marine Fisheries Service Laboratory in Milford, Conn. (64; 155). As the culture techniques were developing, culturists divided them into three distinct phases with differing functions (166). The first phase of clam aquaculture, or the hatchery phase, focuses on the production of ripe brood stock, sperm and egg cells, fertilization, and the culture of the larvae through settlement and metamorphosis. The second, or nursery phase, focuses on the rearing of post-set juveniles to a size in which they become somewhat resistant to predators. The final phase is the grow out phase in which predator resistant–sized animals are grown to market size. A recent book by Manzi and Castagna (167) provides an in-depth review of the fisheries and aquaculture literature as it applies to *Mercenaria mercenaria* and other clam species.

## Hatchery Methods

The hatchery production of seed clams is well established. Most hatcheries divide their operations into four distinct functions: a) algal culture, b) brood-stock maintenance and conditioning, c) larval culture, and d) post-set juvenile maintenance.

Hatchery operations depend on the production of phytoplankton for food for the brood stock, larval, and juvenile clams. There have been a number of excellent reviews outlining the procedures of algal culture (91; 101; 230; 235). In commercial hatcheries, two basic algal culture methods are used. The

*Photograph by Robert Rheault*

Wells-Glancy method relies on the blooms of naturally occurring algal species in nutrient-enriched seawater after initial filtration or centrifugation to remove larger zooplankton (247). The Wells-Glancy method is attractive in that it is simple and inexpensive, but it suffers from the drawbacks of unknown algal species being of variable food quality and being prone to algal die-off or "crashes." Alternatively, if natural food concentrations are high, good larval and juvenile growth can be obtained by pumping large quantities of "raw" seawater past the animals. The Milford method (152; 153) relies on isolated species of phytoplankton in bacteria-free (axenic) cultures, or cultures with few contaminants (oligoxenic). The Milford method of algal production is more labor intensive than the Wells-Glancy method, but there is greater control on food quality (79; 244) and stability of the cultures. Most, but not all, hatcheries now use the Milford method of algal production. A number of hatcheries may use the Wells-Glancy method for production of food for brood-stock maintenance and use the Milford method for producing larval food.

Prior to spawning, quahogs must be fed sufficiently so that gonad growth and maturation can occur. In the natural environment, rising water temperature during the spring months brings algal blooms and the onset of quahog feeding. In a hatchery situation it is often desirable to spawn the animals well before the natural spawning period so that offspring can be set out in the environment early to take advantage of a longer growing period. To condition the brood stock, water temperature must be gradually raised from a maintenance temperature of 12°C (54°F) to about 18 to 20°C (64 to 68°F) and fed an ample supply of phytoplankton. By using a combination of cool storage and conditioning techniques, spawnable brood stock can be made available throughout the year (153; 154).

Spawning of *Mercenaria* can usually be induced by raising the water temperature to between 28 to 30°C (82 to 86°F). If this temperature shock does not work, addition of a suspension of eggs or sperm will frequently induce spawning (51). After spawning, eggs and sperm are mixed to allow fertilization. Following early stages of development, larvae are transferred to a larval culture vessel. Straight-hinge veligers and all subsequent larval stages are fed on phytoplankton. Larval culture vessels will range in size from a few liters to thousands of liters, depending on the size of the facility. Most frequently, commercial hatcheries use 400 to 1,200-liter circular tanks with conical bottoms. Vessels of this size are generally easier to maintain than larger vessels, and it is often wiser to have more medium-sized culture vessels than a few larger ones because many potential diseases can be more easily confined and treated. Typically, larvae are stocked in culture vessels at densities of 1 to 10 larvae/mL and fed algal suspensions at concentrations of

10,000 to 100,000 cells/mL/day. Proper maintenance of larval cultures involves the occasional drain-down of each of the tanks, sieving the larvae to select for the fastest-growing individuals, and cleaning the tanks. At a typical larval-rearing temperature of 25°C (77°F) and with adequate feeding, larvae will be capable of metamorphosis in about eight days. The typical size of metamorphosing *Mercenaria mercenaria* larvae are 190 to 230 µm in length. Under conditions of reduced rations and reduced temperature, metamorphosis can be delayed for up to 20 days (155). Frequently, commercial hatcheries will maintain post-set juveniles for a few weeks in the larval tanks to feed them higher concentrations of algae. Under these conditions, the quahogs will reach 600 µm valve length in two to three weeks. At this time, the quahogs are generally transferred to nursery facilities.

## Nursery Methods

Nursery culture systems provide controlled or semi-controlled conditions for intermediate growth between hatcheries and grow out. As the quahogs grow, their requirement for food grows in proportion to their weight. At the 500 to 600 µm size, it is usually not economically attractive to produce the large quantities of phytoplankton required to maintain the animals in static systems such as the hatchery. The post-set juveniles cannot be planted directly into unprotected field grow out areas without nearly 100 percent loss due to predation (140; 141). There are basically two types of nursery systems: onshore and field. Onshore facilities require the pumping of seawater to deliver sufficient food to the juveniles. Field-based systems usually consist of enclosures and other predator exclusion devices to protect the seed quahogs.

Most frequently, smaller juvenile quahog seed are held in some type of onshore nursery system. In one such system, seawater enters one end, passes the length of the raceway over the quahogs, and exits through a standpipe or spillway drain at the other end. This system is a simple, yet effective, means for rearing early juveniles (51; 102). Another nursery system is called the "upweller" (16; 163; 169) because water flow is actively or passively forced upward through a container holding seed quahogs (Fig. 16). Upwellers are attractive in that they are space efficient. Additionally, the upflow of water from the bottom of the seed quahogs allows for the efficient removal of feces and pseudofeces, thus increasing time between cleanings.

There are a number of field-based nursery systems that have been used successfully. Gravel has been used to protect quahog seed in some bottom nurseries (50; 51). Trays with plastic mesh covers provide excellent protection from predators, but require considerable maintenance due to fouling (77; 148). Off-bottom nursery culture systems utilize a number of devices including rafts, suspended trays, lantern nets, and pearl nets. Recent

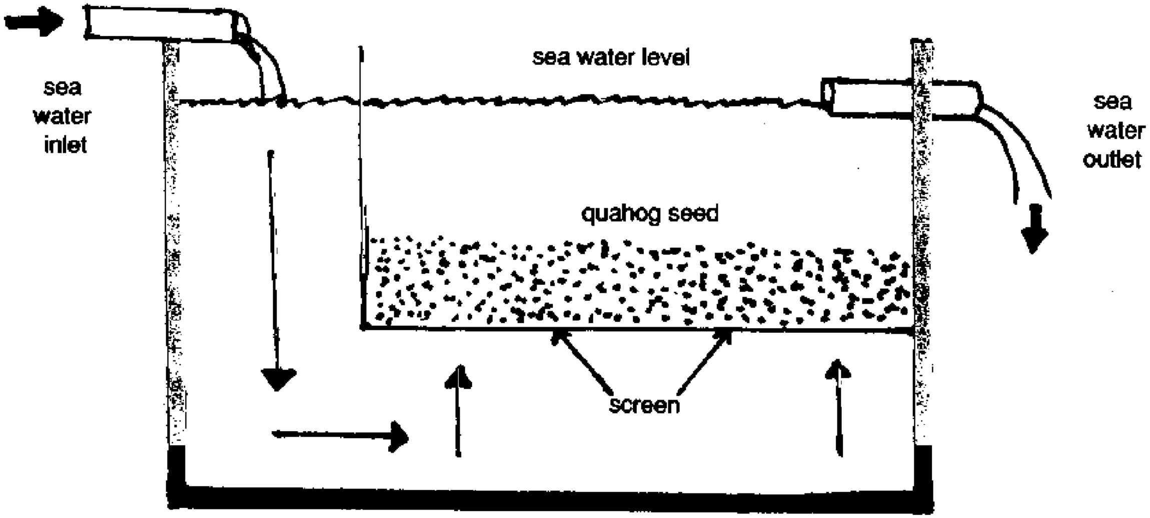


**Figure 16.** Diagrammatic representation of an upweller system for the nursery culture of seed quahogs.

developments in nursery culture systems include a tidal-flow upweller system on a raft (179) and enclosures suspended from floating docks in small-boat marinas (208).

## Grow Out Methods

The technology for raising quahogs from larval to market size in closed recirculating systems has been developed and used in a number of nutrition and other studies (79). One such system utilized treated wastewater (165). For commercial applications, such shore-based facilities have not been economically viable. Most commercial grow out methods currently used are based on field planting intertidally or subtidally with some form of predator protection. Methods of predator exclusion include the use of crushed stone, pens, and net tents (50; 141). Grow out of quahogs in trays provides excellent protection and is used widely (112; 168). It is also known that quahogs can reach market size in shorter time if raised in heated effluents (198).

## Aquaculture Diseases and Pathology

One of the main diseases posed by the culturist is larval vibriosis—a disease caused by bacteria in the genus *Vibrio*. Larval vibriosis can cause 100 percent mortality in larval cultures (35; 78; 234). Cell destruction and tissue death (necrosis) can occur after four to five hours of initial exposure to *Vibrio*. Complete mortality of the larval culture can be within 18 hours. Diagnosis of vibriosis is by culturing on *Vibrio*-specific agar plates, microscopic examination, or a trypan-blue dye exclusion test. Several antibiotics can be used to control vibriosis, but because of the rapid onset of this disease, most hatcheries will simply destroy all infected cultures and carefully disinfect the hatchery (228).

Another disease problem associated with quahog hatcheries is larval mycosis. Larval mycosis is a systemic infection of larvae with the fungus *Sirolpidium zoophthorum* (65; 241). Symptoms of larval mycosis include clumping of larvae and the presence of fungal filaments (hyphae) upon microscopic examination. No known treatment is known for this disease, so infected larval cultures must be discarded. Sinderman and Lightner (229) review the current techniques for disease control in aquaculture systems.

Adult quahogs are susceptible to some other infections. *Chlamydia*-like organisms have been found in quahogs from Chesapeake Bay and the Great South Bay of New York (110; 177), but none of these infections have been associated with severe disease thus far. One study reports a stress response of quahogs associated with pollution and/or shell invasion by the annelid worm *Polydora* (127). It has been reported that some clams may be susceptible to parasites such as *Perkinsus marinus, Hylakossia, Nematopsis*, and *Trichodina* (166); however, direct surveys of cultured and wild *Mercenaria mercenaria* have shown very low incidences of parasitism and histological abnormalities (178). A gonadal neoplasia (cancer) has been described in quahogs from Narragansett Bay, R.I. (253), but incidences of the disease and mortalities have been low (13). It has been suggested that these gonadal neoplasms may be the result of environmental pollution (13). The mechanism for induction of these neoplasms may be a depression of the immune response (4) and subsequent invasion by a viral agent similar to the virus responsible for neoplasms in the soft-shell clam *Mya arenaria* (187).

Although some of the diseases of quahogs resemble human diseases, there is little danger of transmission to the seafood-consuming public. Diseases among shellfish are of greatest concern when they become widespread enough to affect the market supply. So far, the diseases of quahogs have not been widespread or severe enough to be of concern.

# Conclusion

It is hoped that the information presented in this book will be a useful starting point for those interested in understanding the biology and economic value of the northern quahog. The quahog has been important historically, particularly in the Northeast where it has been a food source since pre-colonial times. In Rhode Island, it has even been designated as the official state mollusk. It is highly unlikely that the quahog will become any less important as a food source in the future, now that an emphasis has been placed on promotion of seafoods for their nutritional value. Quahogs, as filter feeders, rely on the natural productivity of estuarine waters to derive their nutrition. They actively filter the abundant phytoplankton for their food and, under proper conditions, grow quickly thereby meeting the demands of a growing seafood market. Aquaculturists are interested in quahogs because supplemental feeds are usually not necessary once they are seeded into estuarine nursery and grow out areas. Fishermen exploit the fast growth of filter-feeding quahogs by being able to harvest productive natural beds on a constant basis. Assuming that fishing effort is not too excessive, or the stocks are well managed, the quahog fishery can be productive well into the future. There is evidence that filter-feeding quahogs are a "natural filter," removing excess phytoplankton produced as a result of increased sewage loading in estuaries. But as filter-feeders, quahogs are quite capable of filtering out and accumulating many of the toxic or disease-causing waste products of our modern industrial society. Maintenance of estuarine water quality is not only good for the quahog, but also for the livelihood of the capture fisheries and the growing aquaculture industries that depend on it. Water quality and the shellfisheries also have important implications to public health. This is because the health of the estuaries, and indeed the quality of life for people living near them, may be reflected by the health of the shellfisheries.

*Photograph courtesy of the* Providence Journal-Bulletin

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