A detailed map of the Chesapeake Bay region, showing the bay's extensive network of rivers and tributaries. Major cities like Washington, Richmond, and Norfolk are marked. The map includes a coordinate grid with longitude (77°00', 76°00', 75°00') and latitude (39°00', 38°00', 37°00') lines. A compass rose is located in the upper left, and a scale bar for nautical miles (0 to 40) is in the lower left. The title and author information are centered over the bay.

Habitat Requirements for the Hard Clam, *Mercenaria mercenaria*, in Chesapeake Bay

Prepared by:
G. Curtis Roegner and Roger Mann
School of Marine Science
Virginia Institute of Marine Science
The College of William and Mary

Special Scientific Report No. 126

December 1990

**Habitat Requirements for
the Hard Clam, *Mercenaria mercenaria*,
in Chesapeake Bay**

**Prepared by:
G. Curtis Roegner and Roger Mann
School of Marine Science
Virginia Institute of Marine Science
The College of William and Mary
Gloucester Point, VA. 23062**

Special Scientific Report No. 126

December 1990

CONTENTS

	Page
Acknowledgments	1
Abstract.	2
Introduction.	3
Background Information.	3
Nomenclature and Taxonomy.	3
Geographic Range	3
Distribution and Population Status	4
Life History.	7
Morphology	7
Spawning and Reproduction.	7
Ecological Role	9
Habitat Requirements.	10
Temperature.	10
Salinity	10
Dissolved Oxygen	11
Turbidity.	11
pH	12
Substrate.	12
Special Problems.	12
Toxicology	12
Toxic Effects of Organic Compounds	13
Toxic Effects of Inorganic Compounds	17
Recommendations	20
Conclusion.	20
Species List	21
Literature Cited.	22

LIST OF FIGURES AND TABLES

	Page
Figure 1. Geographic range of the hard clam in Chesapeake Bay. . . .	5
Table 1. Hard clams densities in the Virginia portion of Chesapeake Bay.	4
Table 2. Toxicity of petroleum products to hard clams.	13
Table 3. Toxicity of polynuclear aromatic hydrocarbons (PAH) to hard clams	14
Table 4. Toxicity of pesticides to hard clam eggs and larvae . . .	15
Table 5. Accumulation and depuration of pesticides by hard clams .	16
Table 6. Toxicity of Surfactants and Syndets to eggs and larvae of hard clams	16
Table 7. Toxicity of inorganic compounds and heavy metals to various life stages of hard clams.	19

ACKNOWLEDGMENTS

This work was synthesized mainly from the species profiles written by Stanley and Dewitt (1983), Stanley, (1985), and Eversole (1987). The annotated bibliographies collected by McHugh et al. (1982) and McHugh and Sumner (1988) were also very helpful. The draft manuscript was improved by critical review by M. Castagna, J. Kraeuter, A.G. Eversole, D. Sved and an anonymous reviewer. Their efforts and contributions are appreciated. Any errors or omissions that remain are solely the responsibility of the authors. Preparation of this report was supported in part by the United States Fish and Wildlife Service.

ABSTRACT

The hard clam, Mercenaria mercenaria, is found along the eastern coast of North America from the Gulf of St. Lawrence to Texas. In Chesapeake Bay the hard clam is restricted to salinities above approximately 12 ppt. The abundances and distribution patterns of hard clams in Chesapeake Bay are based on studies performed nearly 20 years ago - a more extensive survey of hard clam resources is due. Statements concerning long term trends in populations are not feasible.

The basic anatomy of hard clams conform to that of venerid bivalves. Hard clams grow to a maximum shell length (anterior-posterior dimension) of about 120 mm. There are few documented cases of diseases in wild hard clam populations. Parasitic infestations are also slight. The life cycle of the hard clam is typical of other venerid bivalves, and includes a pelagic larval phase and a relatively sedentary benthic juvenile and adult phase. In Chesapeake Bay, ripe gametes can be found between May and October, and spawning commences when temperatures rise above 20-23°C. The larvae are planktotrophic (feeding). Metamorphosis usually commences at a shell length of 200-210µm. Predation on new recruits is very high, dense aggregations of hard clams were found in the absence of predators. Aside from predation and fishing pressure, the natural mortality of larger clams appears very low.

Hard clams are important members of the suspension-feeding infauna. As such they are important in benthic-pelagic coupling, grazing of primary production, transfer of carbon and nitrogen to benthic food chains and, through excretion, rapid recycling of particulate nitrogen as ammonia. The major food source for hard clams is planktonic microalgae. In Chesapeake Bay growth occurs in spring and fall, when optimum water temperatures coincide with abundant food.

Clams are capable of living in a variety of sediment types. Field surveys have often found higher abundances of clams in sandy rather than muddy sediments. A heterogeneous substrate mixture of sand or mud with gravel or shell often show high relative abundances of clams. Hard clam stocks are susceptible to overfishing. Recruitment rates are poorly understood, as are possible reestablishment periods if areas are depleted of clam populations through commercial harvesting. Larval settlement rates and annual recruitment, and the factors that influence these processes, are poorly understood.

Hard clam mariculture is well established and could easily be expanded into sites within the bay.

Given the ability of clams to bioaccumulate toxic substances, an adequate monitoring system should be maintained. The sublethal effects of toxic material readily found in the lower James River should be examined.

INTRODUCTION

The hard clam, Mercenaria mercenaria, is an important member of the suspension-feeding, benthic infauna of lower Chesapeake Bay where it exists in salinities above 12 ppt. Commercially exploitable stocks exist in several areas of the Virginia portion of the bay and have become increasingly important in recent years as watermen look for alternatives to the oyster fishery. The lack of recovery of the oyster fishery dictates that interest in the hard clam fishery will remain at a high level. Comprehensive surveys of the hard clam in the bay are long overdue, much data is over 20 years old. Yet, bayside development continues as does stock exploitation. The purpose of this document is to provide the reader with a broad summary of aspects of the natural history of the hard clam in Chesapeake Bay so that potential impacts of shore line development or other activities in the watershed that eventually have impact on the aquatic environment can be assessed in terms of environmental requirements of the hard clam in the bay.

BACKGROUND INFORMATION

Nomenclature and Taxonomy

Mercenaria mercenaria L. (hard clam, hard-shelled clam, quahog, quahaug, little-necked clam, cherrystone clam, chowder clam, round clam).

Phylum: Mollusca
 Class: Bivalvia
 Subclass: Heterodonta
 Order: Veneroida
 Family: Veneridae
 Subfamily: Chioninae
 Genus: Mercenaria
 Species: mercenaria.
 source: Abbott (1974).

Geographic Range

The hard clam is distributed along the Atlantic coast of North America from the Gulf of St. Lawrence to Florida and along the Gulf of Mexico coast from Florida through Texas (Abbott, 1974; Gosner, 1978). The hard clam has been introduced to California and Europe (Heppell, 1961; Ansell, 1968). The hard clam is restricted to salinities above approximately 12 ppt, and is most abundant in polyhaline estuarine waters. Its bathymetric range extends from the intertidal zone to greater than 18 meters (Gosner, 1978).

In Chesapeake Bay, M. mercenaria is the only common hard clam. Bay-wide surveys of clam populations are limited; however, its potential estuarine distribution is mainly determined by salinity, and it is not abundant below 18 ppt. In the Maryland portion of the bay, hard clam populations are restricted to Pocomoke and Tangier Sounds (Lippson, 1973), although deposits of old shells are found in the lower Patuxent. The bulk of the Chesapeake hard clam distribution is located in the Virginia portion of the bay and subestuarine river systems in salinities exceeding about 12 ppt and depths greater than 5 meters (Andrews, 1970b; Castagna and Chanley,

1973). Hard clams are widely distributed in Chesapeake Bay, but commercially exploitable abundances are limited to an area of about 12,000 acres. These high density distributions are concentrated in the lower York and James rivers (Haven *et al.*, 1973). Limited commercially exploitable abundances are also found in the lower Rappahannock River, Mobjack Bay, and along the western side of the Eastern Shore (Haven, 1970; Haven and Loesch, 1973; Haven *et al.*, 1973).

Distribution and Population Status

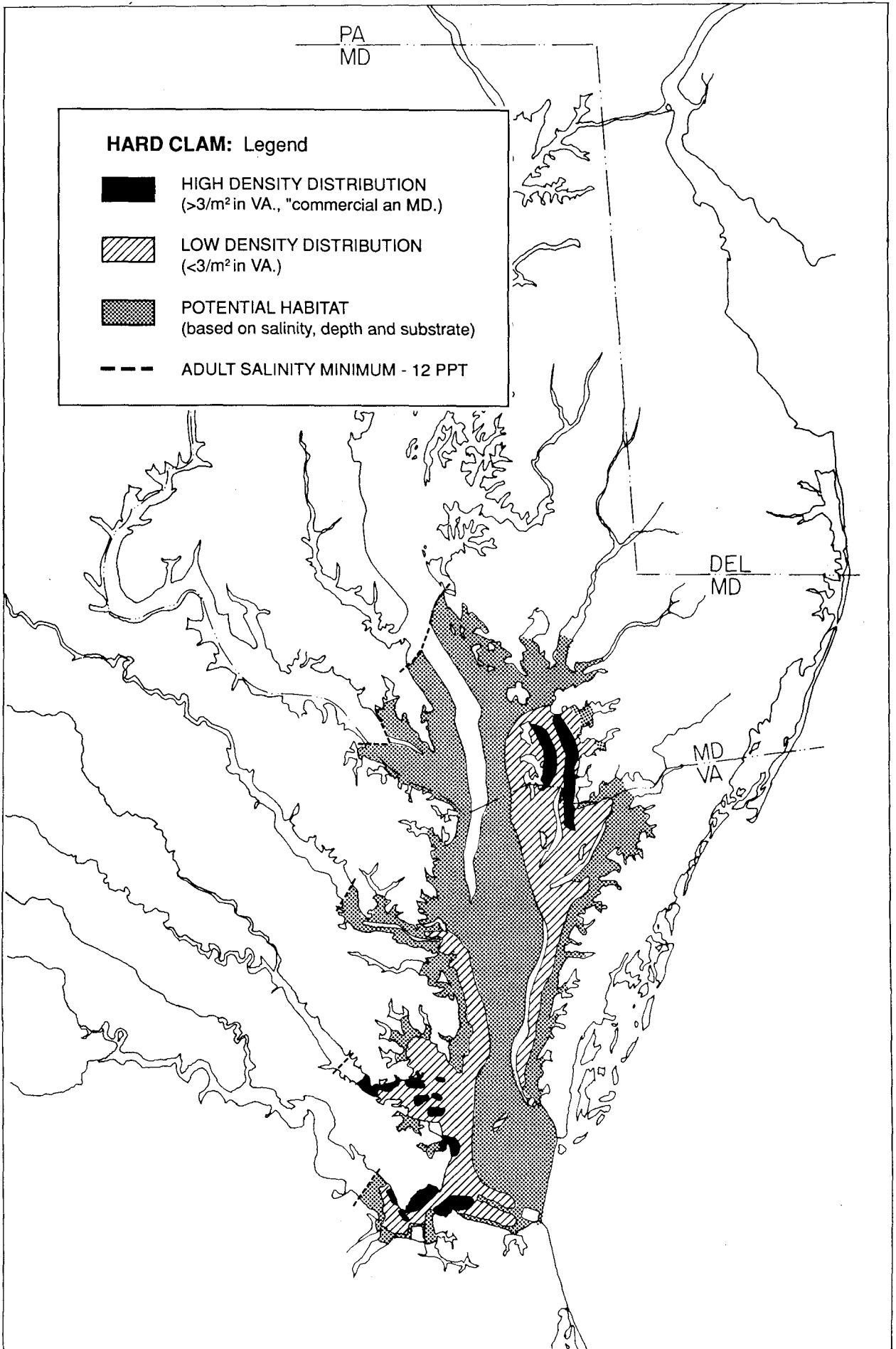
The potential habitat of hard clams in the Chesapeake Bay includes areas where the bottom salinity exceeds 12 ppt, this corresponds to approximately 17 ppt during summer (see Figure 1.) Larval metamorphosis is impeded below 17 ppt (Davis, 1958; Loosanoff and Davis, 1963). Adult hard clams can tolerate salinities to about 12 ppt, but do not grow. Hard clams are capable of small local migrations, pushing out of the sediment and moving with the current. An 18 mm clam can be moved by a 25 cm sec⁻¹ current. The abundance of clams within a habitat is simply the number of larvae that settle minus those removed through post-settlement mortality. The surviving clams may then redistribute in accordance with local currents. Comprehensive studies of larval densities and settlement rates have not been made for Chesapeake Bay sites. Limited data have been reported for areas outside the bay. Carriker (1961) reported 572 larvae l⁻¹ in Little Egg Harbor, N.J., while seed densities as high as 270,000 m⁻² have been recorded in Maine (Dow and Wallace, 1955).

Regular surveys of hard clam resources in Chesapeake Bay have not been made. Statements concerning long term trends in populations are not feasible. Local surveys of hard clam populations in the Virginia portion of Chesapeake Bay reveal population densities varying from 0.7 to 11.1 clams m⁻² (Table 1) The population structure of unexploited populations of hard clams in Chesapeake Bay is usually composed of significantly more larger

Table 1. Hard clams densities in the Virginia portion of Chesapeake Bay.
* from Haven *et al* (1973), ** from Hobbs *et al* (1985).

site	density (clams m ⁻²)
Hampton Bar, James River	8.7-11.1 *
Poquoson Flats	2.4 *
lower James River	0.7-4.7 **
Allens Island, York River	3.9 *
Gaines Point, York River	6.8 *
Mobjack Bay	1.3-2.1 *

Figure 1: Geographic range of the hard clam in Chesapeake Bay



individuals than new recruits or juveniles (Haven et al., 1973; Hobbs et al., 1985). In the bulk of the populations sampled by Haven et al. (1973), greater than 70% of the clams were more than 6 cm in shell length, with an estimated age of 4-8 years. Hobbs et al. (1985) found the highest density of clams smaller than 3.6 cm in shell height (dorso-ventral dimension) to be only 0.44 clams m^{-2} , compared with a density of 3.22 clams m^{-2} for clams larger than 5.8 cm at the same site. In the James River, where densities of adults were among the highest in the bay, the estimated annual recruitment was less than 1 clam m^{-2} (Haven, 1970; Haven et al., 1973). Low recruitment may be the result of high larval mortality, low settlement rates, heavy predation on post settlement forms or some combination of these factors. The hard clam is a long-lived species, and individuals have been aged at more than 30 years (Haskin, 1955; Lutz and Haskin, 1984).

Predation on new recruits is very high, and is known to have eliminated entire sets of both natural and planted stock (Menzel and Sims, 1964; Castagna et al., 1970; Haven and Loesch, 1973; Arnold, 1983; Malinowski and Whitlatch, 1984). Dense aggregations of hard clams were found in the absence of predators (MacKenzie, 1977). In Chesapeake Bay, the blue crab appears to be the primary predator on juvenile hard clams (Haven and Andrews, 1957; Andrews, 1970a; Castagna et al., 1970; Gibbons, 1984), although oyster drills, whelks, and mud crabs are also significant (Andrews, 1970b; Gibbons, 1984). Flatworms can be problematic where clams are cultured out of substrate. The cownose ray is common in Chesapeake Bay (Blaylock, 1989) and is capable of feeding on the larger sizes of hard clams (Andrews, 1970b; Castagna and Kraeuter, 1977). Other important predators include horseshoe crabs, herring gulls, and finfish: tautog, puffer, black drum and flounder (Eversole, 1987). Many predator species prevalent in other areas are prevented from affecting Chesapeake Bay hard clam populations by low salinity (e.g., the sea star).

The size of clams relative to crab size and substrate characteristics interact to form refuges from predation (MacKenzie, 1977; Whetstone and Eversole, 1978; Gibbons, 1984; Gibbons and Castagna, 1985). Crabs feed by crushing small clams and chipping away the edges of larger clams (Stanley, 1985), but clams larger than about 6 cm shell length are immune from most crab predators (Eversole, 1987). Boring gastropods also probably prey more extensively on thinner-shelled, younger individuals. Intense predation intensity on small individuals may explain their poor representation in the size-frequency distributions of populations. Densities of clams are often higher in seagrass beds than in surrounding sand flats (Peterson, 1986), and gravel or shell aggregate has been shown to reduce crab predation (MacKenzie, 1977; Castagna and Kraeuter, 1977; Gibbons and Castagna, 1985). Aside from predation and fishing pressure, the natural mortality of larger clams appears very low (Andrews, 1970b). Eldridge and Eversole (1982) estimate annual mortality to be 1.43% in clams maintained in predator exclusion cages in South Carolina. There are few documented cases of diseases in wild hard clam populations (Sinderman and Rosenfield, 1967), although hard clams in Canada were reportedly decimated by disease (Stewart, 1974). Parasitic infestations are also slight (Eversole, 1987).

LIFE HISTORY

Morphology

Hard clams grow to a maximum shell length of about 120 mm. Abbott (1974) describes the valves of the hard clam as thick, inequilateral, ovate-triangular, and joined at the hinge by a thick brown external ligament. The shell is sculptured with fine concentric ridges that separate and coarsen at the umbones, while at mid-shell the ridges diminish to a characteristic smooth spot. The valves do not gape. A distinguishing external feature is the heart-shaped lunule, located anteriorly to the prominent external ligament. The lunule is typically 3/4 wide as long. Internally, the ventral margin of the shell is crenulate. The hinge architecture is strong, and the anterior and posterior adductor muscle scars and the pallial sinus are prominent. The outer shell of hard clams range in color from yellowish to white, although specimens collected from reduced sediments may be darkly colored. The interior of the shell is usually white tinged with dark purple patches, which were valued by American Indians as wampum (Gosner, 1978). Growth patterns within the shell may reflect the environmental history of the individual (see Lutz and Rhoads, 1980). The basic anatomy of hard clams conform to that of venerid bivalves. The shell-secreting mantle lines the valves and encloses the viscera, and is fused postero-ventrally into the short inhalant (incurrent) and exhalant (excurrent) siphons. The siphons are muscular and retractable and end in tactile and chemosensitive tentacles. The strong, hatchet-shaped foot extends antero-ventrally and is used to burrow into the substrate (Barnes, 1980).

Spawning and Reproduction

The life cycle of the hard clam is typical of other venerid bivalves, and includes a pelagic larval phase and a relatively sedentary benthic juvenile and adult phase (Carriker, 1961; Loosanoff and Davis, 1963).

Sexually, the hard clam is a protandrous and consecutive hermaphrodite and dioecious after changing sex. Sexual maturity is mainly a function of size (Loosanoff, 1937a, 1937b; Quayle and Bourne, 1972; Bricelj and Malouf, 1980). Clams develop functional male gonads at 6-7 mm in shell length in the first or second year of life. Oocytes are sometimes present at this time. After this juvenile male phase definitive sexes are established at a size of about 30 mm shell length (Loosanoff, 1936, 1937a; Ansell, 1967; Eversole, 1987). Spawning cycles are mainly affected by temperature and food availability, and thus vary according to latitude. Spawning often occurs in pulses and may continue for months (Davis and Chanley, 1956), but usually there are one or more distinct spawning peaks; a second spawning peak often occurs from North Carolina south (Adamkewicz, 1987; Eversole, 1987). When ripe gametes have been produced, spawning is stimulated by a temperature increase over some threshold. In Chesapeake Bay, ripe gametes can be found between May and October (Chanley and Andrews, 1971), and spawning usually commences when temperatures rise above 20-23°C (Andrews, 1970b; M. Castagna, pers. comm.).

Fecundity in hard clams is high. Females can release between 16 and 24 million eggs per spawn (Davis and Chanley, 1956) although laboratory studies

have often recorded lower values of 1 to 3 million (see Knaub and Eversole, 1988). With repeated spawns individuals may release up to 60 million eggs over a season. The viability of eggs and subsequent survival of larvae are positively related to egg size but not clam size (Loosanoff *et al.*, 1953; Ansell, 1967; Kraeuter *et al.*, 1981); however, the amount of spawn released increases with increasing clam size (Bricelj and Malouf, 1980). Carriker (1961) reports that eggs are 60-85 μm in diameter when released and covered with a gelatinous membrane that expands on contact with water, further extending the diameter to 163-179 μm (Carriker, 1961). In culture experiments, however, eggs will often pass through a 35 μm mesh but are retained on a 25 μm mesh. Fertilization occurs in the water column.

The larvae of hard clams are planktotrophic (feeding) and development of the larval forms follows the usual blastula, gastrula, trochophore, straight-hinged (90-140 μm), umboned (140-220 μm), and pediveliger (170-230 μm) stages of bivalve molluscs (Loosanoff and Davis, 1963; Chanley and Andrews, 1971). Rate of development is highly dependent on temperature, salinity, availability of high quality food and turbidity (see below), but under optimum conditions the larval stage can be completed in as little as a week (Loosanoff, 1959). On the other hand, the larval stage can be maintained for at least 24 days if conditions are inadequate or suitable substrate is lacking (Loosanoff, 1959).

Mature pediveliger larvae have a well developed, ciliated foot and byssus gland in addition to a functioning velum (Carriker, 1961). The pediveligers alternate swimming with crawling on the bottom using the foot, and this behavior facilitates testing the substrate for suitable settling sites. Pediveligers can distinguish between different sediment types, although the selective mechanisms involved are unclear (Keck *et al.*, 1974). Distribution of larvae within the estuarine system is probably a combination of active site regulation and passive deposition (Wood and Hargis, 1971; Butman *et al.*, 1988). During settlement, the pediveliger anchors itself to the substrate with a byssal thread terminating the period of planktonic life (Carriker, 1961). It is unclear whether the velum is absorbed or cast off at settlement. Degeneration of the velum may precede settlement. The ciliated foot of the pediveliger also serves as a swimming organ. The settled clam is now termed a byssal plantigrade, which slowly metamorphoses into a juvenile clam. Metamorphosis entails the development of the digestive viscera and gills, the fusion of the mantle edges, and the development of the siphons, and is a gradual processes. Metamorphosis usually commences at a shell length of 200-210 μm (Loosanoff and Davis, 1963).

Young byssal plantigrades initially lie at or just under the sediment surface, but can move about on the foot while the byssal threads can be alternately detached and reformed. The exhalant siphon is usually developed at metamorphosis but the inhalant siphon does not usually appear until a length of approximately 1.5 mm. As the siphons develop and elongate, the byssal plantigrade burrows progressively deeper into the substrate. The siphons initially maintain contact with the overlying water, but after the formation of siphonal tentacles, which aid in the exclusion of sediment from the inhalant stream, the clam may be completely buried. At a shell length of about 7-9 mm, the byssal gland is lost and the byssal plantigrade becomes

a juvenile plantigrade. Mobility is effected by the shortened, hatchet-shaped foot (Carriker, 1961).

ECOLOGICAL ROLE

Hard clams are important members of the suspension-feeding infauna. As such they are important in benthic-pelagic coupling, grazing of primary production, transfer of carbon and nitrogen to benthic food chains and, through excretion, rapid recycling of particulate nitrogen as ammonia. The major food source for hard clams is planktonic microalgae. Normally, clams lie buried in the substrate with only the siphons communicating with the surface. Specialized gill cilia draw a respiratory and feeding current down the inhalant siphon, through the gills, and out the exhalant siphon. Food particles brought in by the inhalant stream are filtered out by cilia and trapped in mucus strings, and are transported to the labial palps, where the material is sorted by size. Organic and inorganic particles in the size range of about 5 to 15 μm are imbedded in mucus strings and ingested. Material rejected from the sorting cilia on the gills or labial palps is concentrated near the base of the inhalant siphon and periodically ejected by forceful adductions of the valves. This material is called pseudofeces. The sensory tentacles on the inhalant siphon can reduce the aperture to limit inhalation of sediment.

Filtration rates of hard clams are related to food concentration. Feeding efficiency increases with increasing particle density until a maximum, and then decreases at higher levels (Tenore *et al.*, 1973). Optimum algal density for hard clam filtration is 2×10^5 cell ml^{-1} (Tenore and Dunstan, 1973). Clams have been measured to assimilate 71.2-77.3% of the ingested food (Tenore *et al.*, 1973). Walne (1972) found maximum filtration rates were dependent on the species of algae. Feeding rate also increased directly with temperature and current velocity (Walne, 1972).

The hard clam exhibits seasonal, latitudinal, and size related variations in growth (Ansell, 1968; Eversole *et al.*, 1986). In warm-temperate areas such as Chesapeake Bay, the most significant growth occurs in spring and fall, when optimum water temperatures coincide with abundant food (see section on Environmental Requirements). Growth decreases in summer, and ceases during winter (at water temperatures less than 9°C). Seasonal growth increments increase along the north-south latitudinal gradient; thus clams grow to market size earlier in areas with longer growing seasons (Ansell, 1968). Growth rate also tends to decrease with age (Pratt and Campbell, 1956; Eversole *et al.*, 1986). As growth ceases with either old age or adverse conditions, clams become thicker ("blunt") rather than increasing in shell length.

Hard clams exhibit a wide geographical variation in growth rate. On Hampton Flats, growth modeling estimates indicate 2.5 years are needed to reach a size of 3.8-5 cm, and 4.5 years to reach a size >6 cm, while in the lower salinity areas of York River, 4-5 and 8 years are required for the respective size classes. Chowder size clams at the same locations were estimated to be 8-20 years old (Haven, 1970; Haven and Loesch, 1973; Loesch and Haven, 1973).

HABITAT REQUIREMENTS

Temperature

Temperature affects hard clam reproduction and growth of larvae and adults. Gametogenesis begins when water temperatures reach about 10°C (Eversole, 1987), and temperature is one of the main stimuli for spawning in the hard clam. Critical spawning temperatures vary along a geographic transect because of acclimation of populations to local conditions (reviewed in Knaub and Eversole, 1988). In Chesapeake Bay, spawning usually begins in May when water temperatures rise above 23°C (Jefferies, 1964; Kennedy et al., 1974).

Younger life stages generally have narrower temperature tolerances for survival than adults. Eggs remain viable from 7.2-12.5°C to over 32.5°C (Davis and Calabrese, 1964; Lough, 1975; Kennedy et al., 1974), but embryos and trochophores at temperatures >30°C experienced increased mortality with increased exposure time (Kennedy et al., 1974). Larvae survived temperatures between 12.5 and 30.0-33°C (Carriker, 1961; Loosanoff and Davis, 1963); the best survival was between 22.5-25.0°C at 22.5 ppt salinity (Davis and Calabrese, 1964). Adult hard clams can survive temperatures between -6°C and 45.2°C. (Henderson, 1929; Williams, 1970). Activity of adults is curtailed below 1°C and above 34°C (Hamwi, 1968; Van Winkle et al., 1976) and optimal between 21°C and 31°C (Savage, 1976).

Larval growth and survival are functions of both temperature and salinity (Davis and Calabrese, 1964; Lough, 1975). Growth of larvae ceases at <12.5°C (Loosanoff and Davis, 1963) mainly because the larvae cannot assimilate ingested food (Davis and Calabrese, 1964). Davis and Calabrese (1964) determined the optimum temperature for growth for most salinities (<27.0 ppt) to be 25-30°C. Lough (1975) determined the optimum temperature range for larval growth from fertilization to 10 days at 21.5-30 ppt salinity to be 22.5-36.6°C. Temperature also affects the developmental rate of larvae. Loosanoff (1959) reported the time between fertilization and settling to be 20 days at 18°C (16-24 d) and 7.5 days at 30°C (7-9 d). Growth of adults occurs between 8°C and about 31°C (Ansell, 1968; Belding, 1931), with an optimum temperature of 20°C (Ansell, 1968; Pratt and Cambell, 1956). The latter values are below those quoted earlier from Savage (1976) and probably reflect inhibition of bacterial activity at the lower temperatures.

Salinity

Salinity significantly affects both growth and survival of hard clams. Larval forms are more sensitive to adverse salinity levels than are adults. The salinity range for normal egg development is 20-35 ppt (Davis, 1958;

Davis and Calabrese, 1964) with an optimum of about 27 ppt (Loosanoff and Davis, 1963). High mortality occurs at <12-17 ppt (Chanley, 1958; Loosanoff and Davis, 1963; Castagna and Chanley, 1973). The upper and lower salinity limits for normal larval development are 15-35 ppt, thus larvae can exist in lower salinity regimes more successfully than eggs (Loosanoff and Davis, 1963). Metamorphosis, however, is inhibited at <17 ppt (Davis, 1958; Loosanoff and Davis, 1963). Optimum salinity for growth and survival to settlement is 26-27 ppt (Davis, 1958; Loosanoff and Davis, 1963; Davis and Calabrese, 1964; Castagna and Chanley, 1973).

The synergistic effect of salinity and temperature on larval growth and survival results in a limiting of the ranges of temperature tolerance with a reduction in salinity, especially at high temperatures and low salinities (Davis and Calabrese, 1964). Thus higher mortalities and slower growth of larvae are expected at <17.5 ppt. The minimum salinity tolerance for adults is approximately 12 ppt while clams can exist in waters of oceanic salinities (Stanley, 1985) and above. For example, hard clams have been recorded in Laguna Madre, Texas at salinities of up to 48 ppt! The ability of hard clams to tightly adduct the valves reduces the negative effects of short term environmental fluctuations. Reproduction is inhibited at <15 ppt (Castagna and Chanley, 1973). Thus salinity is a major factor in hard clam distribution patterns. In Chesapeake Bay, clams are not abundant at <20 ppt (Andrews, 1970b; M. Castagna, pers. comm.).

Dissolved Oxygen

Dissolved oxygen (DO) is not usually a limiting factor to hard clams in Chesapeake Bay. Anoxic events are usually concentrated in lower salinity, upper bay areas outside the salinity tolerance for metamorphosis or in deeper regions where clams are scarce. Additionally, clams of all life stages exhibit a marked tolerance to low DO. The minimum DO requirement for normal development is about 0.5 mg l^{-1} , although growth rates are greatly reduced below 4.2 mg l^{-1} (Morrison, 1971). Short-term stress does not affect later development (Morrison, 1971). Adult hard clams can maintain oxygen consumption down to DO levels of 5.0 mg l^{-1} , after which oxygen consumption declines and, presumably, anaerobic metabolism becomes responsible for a greater proportion of total metabolic activity (Hamwi, 1968, 1969). DO levels $<5.0 \text{ mg l}^{-1}$ clearly represent stress to hard clams. Activity can be maintained even at DO levels $<1.0 \text{ mg l}^{-1}$ (Savage, 1976).

Turbidity

Heavy sediment loads have negative effects on growth and survival, although clams can usually tolerate ambient concentrations of suspended materials. Eggs suffered increasing abnormal development with increasing silt concentration from 0.75 g l^{-1} to 3 g l^{-1} , when no normal development ensued (Davis, 1960). Larvae were not able to survive or grow in concentrations of 0.25 g l^{-1} chalk or 0.50 g l^{-1} of Fuller's earth, although eggs could withstand higher levels (Davis, 1960; Davis and Hidu, 1969b).

Growth of larvae was inhibited in silt concentrations above 0.75 g l^{-1} ; however, survival was high even at 4 g l^{-1} (Davis, 1960; Davis and Hidu, 1969b). High concentrations of small particles tended to clog the larval alimentary tract (Davis and Hidu, 1969b). Juvenile and adult clams (14 and 32 mm shell length) decreased the ingestion rate of algae with increasing sediment load (up to 0.044 g l^{-1}), and lost 18% of ingested algae by increased production of pseudofeces (Bricelj and Malouf, 1984). The rate of filtration was also depressed by additions of silt (Rice and Smith, 1958). Growth of hard clams was inhibited at 0.044 g l^{-1} but not at 0.025 g l^{-1} (Bricelj *et al.*, 1984). Most of these detrimental concentrations are higher than those encountered in nature, except perhaps during dredging or very heavy runoff events.

pH

marine and estuarine waters are usually well buffered. Hard clams are tolerant of most pH levels commonly encountered in their habitat. Embryos developed normally at pH values of 7.00-8.75, while larvae survived in the range 6.25-8.75 (Calabrese and Davis, 1966; Calabrese, 1972). Growth occurred between 6.75-8.50, with an optimum between 7.50-8.50 (Calabrese and Davis, 1966; Calabrese, 1972).

Substrate

Substrate characteristics are important for hard clam growth, distribution, and abundances. Larvae prefer to settle in sand over mud substrates, but particle size was not deemed an important factor (Keck *et al.*, 1974). Clams are capable of living in a variety of sediment types. Field surveys have often found higher abundances of clams in sandy rather than muddy sediments; however, this varies by location (Allen, 1954; Wells, 1957; Anderson *et al.*, 1978). A heterogeneous substrate mixture of sand or mud with gravel or shell often show high relative abundances of clams (Pratt, 1953; Taxiarchis, 1955). This appears to relate to the larger material offering a spatial refuge from predation (Arnold, 1983). Higher growth rate has also been observed in sand substrate (Chestnut, 1951; Pratt and Cambell, 1956; Lutz and Rhodes, 1980; Grizzle and Morin, 1989).

SPECIAL PROBLEMS

Toxicology

The toxic action of a number of organic and inorganic compounds on hard clams has been investigated. The ability to culture hard clams has allowed for the evaluation of many compounds on the larval stages. Embryos and larvae are much more susceptible to toxicants than are the adults. The adults can often withstand large body burdens of toxic materials, and can concentrate such substances far above ambient conditions. Additionally, the depuration of such compounds is often slow. This is of obvious concern since hard clam populations, especially in the James River, are often subjected to toxicants. One important aspect of pollution biology is sublethal effects (e.g., reduction of reproductive output); such effects are

poorly understood. The following section on toxicants uses values of LC50 and EC50. These are defined as follows:

LC50 = Concentration causing death of 50% of the test organisms.

EC50 = Concentration affecting specific response in 50% of test organisms (i.e., growth).

Toxic Effects of Organic Compounds

Concentrations of petroleum products in the low ppm range are toxic to embryonic and larval clams (Table 2). Such concentrations have been directly measured in the field following a spill as well as experimentally determined in a oil spill weathering simulator (Byrne and Calder, 1977). Growth studies using EC50 values indicate that petroleum products decrease growth rates when compared to controls (Byrne and Calder, 1977). This sublethal effect is important because increased mortality is usually associated with increased planktonic existence. The hard clam is very sensitive to waste motor oil, which makes up a significant portion of petroleum pollution (Byrne and Calder, 1977).

Hydrocarbon depuration is slow. Adult hard clams depurated only about 30% of accumulated hydrocarbons in 120 days (41.9 ppm to 29.3 ppm wet weight) (Boehm and Quinn, 1977). Shelton (1971) describes clams with initial contamination levels of benzo(a)pyrene of 16.0 ppb reducing body burden to 8.2 ppb after 7 weeks and having a residual of 1.1 ppb after 60 weeks. Oiled sediments reduce the depth to which clams bury while increasing burial time (Olla *et al.*, 1983).

Polyaromatic hydrocarbons (PAHs) were found to accumulate in hard clams much faster than they were depurated, giving bioaccumulation factors in the 10^3 - 10^4 range (Bender *et al.*, 1988) (Table 3); however, oysters were found to have even higher bioconcentration factors because of their significantly lower depuration rates compared to hard clams (Bender *et al.*, 1988).

Table 2: Toxicity of petroleum products to hard clams. Data from Byrne and Calder (1977). All LC50 and EC50 values in ppm.

	Embryo	Larvae					
		48-h LC50	LC50			EC50	
			48-h	144-h	240-h	144-h	240-h
Kuwait Crude	12	25	13.1	2.0	15.7	4.2	
Southern Louisiana Crude	5.7	6.0	5.3	2.1	3.2	1.1	
Bunker C	1.0	3.2	1.8	1.6	1.9	1.0	
No. 2 Fuel Oil	0.43	1.3	1.3	0.53	0.63	0.57	
Florida Jay Crude	0.23	0.25	0.11	0.55	0.29	0.22	
Used Motor Oil	0.04	0.10					

Table 3: Toxicity of polynuclear aromatic hydrocarbons (PAH) to hard clams.
Data from Bender et al. (1988)

Bioconcentration test: 28-d accumulation and 28-d clearance rates (ppm/d).

Compound	Uptake Rate	Clearance Rate	Bioconcentration Factor
Benzo(a)anthracene	2824	0.172	16516
Benzo(a)fluorine	994	0.167	5943
Benzo(b)fluorine	1190	0.162	7332
Benzo(a)pyrene	361	0.087	4143
Benzo(e)pyrene	2366	0.148	15980
Benzo(ghi)fluranthene	3384	0.145	23306
Benzofluoranthene	1857	0.180	10331
Chrysene	1190	0.162	7335
Flouranthene	1477	0.213	6934
Methylphenanthrene	187	0.115	1628
Methylpyrene	2002	0.148	13571
Perylene	1133	0.161	7059
Phenanthrene	224	0.114	1974
Pyrene	1587	0.194	8172
Total PAH	556	0.137	4072

Table 4: Toxicity of pesticides to hard clam eggs and larvae. Data from Davis (1961) and Davis and Hidu (1969a).

Compound	48-h LC50 Eggs (ppm)	12-d LC50 Larvae (ppm)
Insecticides		
Aldrin	>10	0.41
Co-Ral	9.12	5.21
Dicapthon	3.34	5.74
Di-Syston	5.28	1.39
Guthion	.86	.86
Lindane	>10	>10
N-3514	<1	<1
Sevin	3.82	>2.50
Toxaphene	1.12	<.25
Herbicides		
Diuron	2.53	>5
Endothal	51.02	12.50
Fenuron	>10	>5
Monuron	>5	>5
Neburon	<2.4	<2.4
Nematocide		
Nemagon	10	.78
Solvents		
Acetone	>100	>100
Allyl alcohol	1.03	<.25
Orthodichlorobenzenz	>100	>100
Trichlorobenzene	>10	>10
Bacteriocides, Algicides		
Fungicides, ect.		
Chloramphenicol	74.29	50
Delrad		0.072
Dowicide A	>10	0.75
Dowicide G	<0.25	<0.25
Griseofulvin	<0.25	<1
PVP-Iodine	17.10	34.94
Nabam	<0.50	1.75
Nitrofurazone	>100	>100
Omazene	0.081	0.378
Phenol	52.63	55.00
Phygon	0.014	1.75
Roccal	0.19	0.14
Sulmet, tinted	>100	>100
Sulmet, untinted	>1000	>1000
TCC	0.032	0.037

Table 5: Accumulation and depuration of pesticides by hard clams.
References 1: Butler, 1964; 2: Butler, 1966; 3: Eisler and Weinstein, 1967; 4: Courtney and Denton, 1976; 5: Huggett, et al., 1980; 6: Becerra-Huencho, 1984; 6: Roberts, 1987

Compound	Life Stage	Test/Dose	Results	Ref
DDT	Adult	Dose = 1 ppb	Accum = 3-9 ppm	1
		Depuration:	0d 3.5 ppm	
			10d 0.88 ppm	
			20d 0.161 ppm	
		Dose = 7d @ 1 ppb	Accum = 6 ppm.	2
Kepone	Adults	Depuration:	15d 0.5 ppm	
		Dose = 18d @ 0.0125 ppm	Accum = 10.0 ± 5.8 ppm	5
Tributyltin Oxide (TBTO)	Embryo	Mean residue = 0.09 ppm		6
		24-h LC50 > 1.31 ppb		7
Oxide (TBTO)	Larvae	48-h LC50 = 1.13 ppb (0.72-1.31 ppb)		7
		24-h LC50 > 4.21 ppb		7
		48-h LC50 = 1.65 ppb		7
		96-h LC50 = 0.015 ppb		6
Methoxychlor	Adults	Dose = 4 ppb	Accum: 1.3 ppm gills	4
			0.075 ppm mantle	

Table 6: Toxicity of Surfactants and Syndets to eggs and larvae of hard clams. Data from Hidu (1965). All LC 50 and EC 50 values are ppm unless otherwise specified.

Compound	Life Stage	LC50 (range)	EC50	
Anionic				
Alkyl Aryl Sulfate	egg + larvae	1.55 (0.55-3.00)		
			AAS-1	5.83
			AAS-2	0.98
AAS-3	1.03			
Alkyl Sulfate	egg + larvae	1.22 (0.73-1.46)		
			AS-1	0.47
Cationic	egg + larvae	0.34 (0.01-1.00)		
			C-1	1.27
C-2		0.85 ppb		
Nonionic				
N1	egg + Larvae	2.66 (1.00-5.00)		
				0.77
N2			1.75	

In contrast to the relative tolerance levels of temperature and salinity on the early life stages of hard clams, the toxicity of the pesticides, herbicides, bacteriocides, and fungicides tested by Davis (1961) and Davis and Hidu (1969a) were usually greater for larvae than eggs (Table 4). The relative LC50 values of the compounds vary, but are generally in the ppm range (Davis, 1961; Davis and Hidu, 1969a). Some compounds (Sevin, Endothal, 2-4-D salt, phenol, and Sulmet) accelerated larval growth over controls; the reason is unclear but antibiotic properties or chelation of toxics were suspected. Except for allyl alcohol, the organic solvents tested were not toxic (Davis and Hidu, 1969a).

Hard clams concentrate pesticides, but do not store polychlorinated hydrocarbon pesticides as well as other species (Table 5). Accumulation was slower and depuration of a variety of pesticides was faster in hard clams than in the soft shell clam (Butler, 1971, 1973). When exposed for 18 days to a DDT

concentration of 1.25 ppb, mean concentration of contaminant in hard clam tissue exceeds the environmental concentration by a factor of 1.8×10^3 , with slightly over 3 months being required for depuration (Courtney and Denton, 1976). Butler (1966) reported accumulations of 6 ppm after 1 week at a DDT concentration of 1 ppb. At higher concentrations, DDT decreased in foot tissue after 6 months while the concentration in the viscera did not measurable decrease (Courtney and Denton, 1976). The concentration of DDT in hard clams in Long Island, NY was found to be 0.42 ppm (Woodwell *et al.*, 1967). Fortunately, DDT use is now banned in the United States.

Tributyltin (TBT) was found to be highly toxic to hard clam eggs and larvae, with LC50 values in the parts per trillion range for eggs and embryos, and the ppb range for larvae and juveniles (Roberts, 1987). A concentration of 0.77 ppb tributyltin chloride depressed growth rates, although the resultant larvae were normal (Roberts, 1987).

Kepone contamination of the James River estuary was recognized in 1975, and the substance was found to be present throughout the food chain. Hard clams had comparatively low concentrations of the insecticide, and no directly toxic effects were discovered (Huggett *et al.*, 1980).

The sublethal effects of chlorinated hydrocarbon contamination include depressed glucogenesis and enhanced glucose degradation. This indicates stress in the organism (Engle *et al.*, 1972). Other enzyme pathways may be affected (Engle *et al.*, 1972).

Hidu (1965) found hard clam embryos and larvae to have relatively low tolerances to surfactants (Table 6). Values for the 48 h LC50 ranged between 0.0085-5.83 ppm; actual field concentrations of surfactants in the St. Mary's River, Maryland have been reported at 0.06 ppm (Hidu, 1965). Again, clam larvae were more tolerant than oyster larvae. Eisler *et al.* (1972), in contrast, found sodium nitrilotriacetic acid (NTA) to be non-toxic to adult oysters. Values for the 168 h LC50 were more than 10 ppt. Hard clams were the least sensitive species examined.

Toxic Effects of Inorganic Compounds

Juvenile and adult clams were relatively unaffected by high concentrations of ammonia and nitrite, while nitrate and orthophosphate had

no deleterious effects (Epifanio and Snra, 1975) (Table 7). The lethal values for these compounds are higher than are normally encountered. In contrast, chlorine was highly toxic to hard clam larvae, with EC50 values near the ppb level (Roberts et al., 1975; Scott and Vernberg, 1979).

Heavy metals were toxic to eggs and larvae of hard clams in the ppb to ppm range (Calabrese and Nelson, 1974; Calabrese et al., 1977a, 1977b, 1982). Metals are known to be concentrated in hard clams at several magnitudes greater than the surrounding environment. Accumulation and depuration rates are dependent on such physical factors as temperature and salinity, which affect metabolic rates (Pringle et al., 1968). In hard clams taken from Southampton, England, metal accumulation was inversely related to salinity, but little correlation was found between sediment metal and tissue metal concentrations (Romeril, 1979). Generally, depuration rates of heavy metals from hard clams are slow. Levels of Cd, Cr, Ni, Pb, Zn, and Cu either remained the same or increased after transplantation from a polluted area in Great South Bay, N.Y. (Behrens and Duedall, 1981). Accumulation rates, body burdens, and depuration rates of heavy metals in hard clams are low relative to oysters and soft clams (Pringle et al., 1968). Oxygen consumption rates increased with increasing Ag concentrations (Thurberg et al., 1974).

Heavy metal toxicity varies with life stage and type of metal. Early life stages are more sensitive to Hg and Ag than Cd, possibly because of lower accumulation rate for Cd, but the order is reversed in older animals, perhaps because of tolerance to Hg and Ag (Calabrese et al., 1977a). Shuster and Pringle (1968) found the relative toxicity of metals to hard clams to be $Cu > Cd > Cr > Zn$, while Calabrese et al. (1977b) determined metal toxicity to larvae to be $Hg > Cu > Ag > Zn > Ni$ (Ni was relatively nontoxic). Metal concentrations also increased with age of clams, probably reflecting the extended exposure of the older animals to the toxicant (Romeril, 1979).

In Chesapeake Bay, Larsen (1979) examined levels of Cd, Cu and Zn in hard clams from the James and York rivers and several sites in Chesapeake Bay. The levels of these metal was found to variable within samples (Zn at 5.0-112 ppm, Cu at 1.0-16.5 ppm, and Cd at <0.8 ppm) but were generally comparable with other studies; however, the metal content was higher in the James River than in the York River or bay proper, suggesting heavy metal contamination in the James River (Larsen, 1979).

Table 7: Toxicity of inorganic compounds and heavy metals to various life stages of hard clams. References: 1: Epifanio and Srna, 1975. 2: Roberts et al., 1975. 3: Scott and Vernberg, 1979. 4: Pringle et al., 1968. 5: Calabrese and Nelson, 1974. 6: Thurberg et al., 1974. 7: Calabrese et al., 1977a. 8: Calabrese et al., 1977b.

Compound	Life Stage	Test/Dose	Comments	Reference
Ammonia	Juveniles and Adults	96-h LC50 = 110-172 ppm		1
Nitrite	Juveniles and Adults	96-h LC50 = 81-85 ppm		1
Chlorine	Larvae	48-h EC50 = 6 ppb		2
		48-h EC50 < 6 ppb		3
		48-h LC50 = 1 ppb		2
Ag	Embryo	48-h LC50 = 0.021 ppm		5
		48-h LC100 = 0.045 ppm		5
	Larvae	10-d LC5 = 0.0186 ppm		8
		10-d LC50 = 0.0324 ppm		7,8
		10-d LC95 = 0.0462 ppm		8
		% Growth @ LC95 = 66.2		8
Adult	96-h Dose @ 0.100 ppm	Ag accumulation in gills, increased oxygen consumption		
Cu	Larvae	10-d LC5 = 0.0049 ppm		8
		10-d LC50 = 0.0164 ppm		7,8
		10-d LC95 = 0.0280 ppm		8
		% Growth @ LC50 = 51.7		8
	Adult	Dose @ 0.5 ppm, Accum rate = 0.06g/kg/day		4
		84-d Depletion rate = 50 ppm/d		4
Fe	Adult	84-d: no depletion observed		4
Hg	Embryo	48-h LC50 = 0.166 ppm		5
		48-h LC100 = 0.0075 ppm		5
	Larvae	10-d LC5 = 0.004 ppm		8
		10-d LC50 = 0.0147 ppm		7,8
		10-d LC50 = 0.0147 ppm		8
		10-d LC95 = 0.0254 ppm		8
		% Growth @ LC50 = 68.7		8
Adult	84-d Depletion rate = 120 ppm/d		4	
Mn	Adult	84-d Depletion rate = 95 ppm/d		4
Ni	Embryo	48-h LC50 = 0.31 ppm		5
		48-h LC100 = 0.60 ppm		5
Pb	Embryo	LC100 = 1.2ppm		5
	Adult	Dose = 0.2ppm Accum rate = 0.63g/kg/day		4
Zn	Embryo	LC50 = 0.166 ppm		5
		LC100 = 0.25 ppm		5
	Larvae	10-d LC5 = 0.050 ppm		8
		10-d LC50 = 0.1954 ppm		8
		10-d LC95 = 0.3410 ppm		8
	% Growth @ LC50 = 61.6		8	

RECOMMENDATIONS

- 1) Resource management requires a firm knowledge of the the resource. Abundance and distribution patterns of hard clams in Chesapeake Bay are based on studies performed nearly 20 years ago. A more extensive survey of hard clam resources is due. Early life history of hard clams in the bay has not been investigated. Larval settlement rates and annual recruitment are poorly understood. Basic research is needed.
- 2) Hard clam stocks are susceptible to overfishing. Recruitment rates and reestablishment periods for depleted areas are poorly understood. Hydraulic dredges are efficient harvest mechanisms capable of eliminating the bulk of the clams in an area. Patent tongs are less efficient. Control of the method of harvest is a prudent measure to control fishing mortality.
- 3) Hard clam mariculture is well established and could easily be expanded into sites within the bay, although site specific salinity may influence growth and economic viability. Mariculture offers a direct alternative for employing watermen and conserving the natural resource.
- 4) Hard clams can accumulate toxic substances. An adequate monitoring system should be maintained. The sublethal effects of toxic material readily found in the lower James River should be examined.

CONCLUSION

The hard clam is an important member of the suspension feeding infauna and contributes significantly to grazing of single cell plankton, benthic pelagic coupling and nutrient recycling in the bay. The hard clam also supports a significant commercial industry. Yet, information on hard clam distribution and abundance is outdated or lacking. Early life history, especially recruitment, processes in the bay are very poorly understood and present problems for effective management. Appropriate survey and research needs are obvious. Salinity limited distribution of hard clam stocks in the bay spatially separates them from areas most subject to low dissolved oxygen events. Nonetheless hard clams have only limited tolerance to low dissolved oxygen stress and will be the subject of concern if spatial distribution of seasonal hypoxia threatens to extend beyond its present limits. A large body of information on toxic effects of a number of organic and inorganic compounds on hard clams underscores the need to reduce disposal of such materials into the bay ecosystem. The hard clam is a suitable candidate for mariculture and is unusually free of natural diseases and parasites. Mariculture of hard clam should be encouraged.

SPECIES LIST

Throughout the preceding text common names have been used. For comparison the latin or scientific names are given below.

common name	latin name
black drum	<u>Pogonias cromis</u>
blue crab	<u>Callinectes sapidus</u>
cownose ray	<u>Rhinoptera bonasus</u>
flatworm	<u>Stylochus ellipticus</u>
flounder	<u>Paralichthys dentatus</u>
herring gulls	<u>Larus argentatus</u>
horseshoe crabs	<u>Limulus polyphemus</u>
mud crab	<u>Eurypanopeus depressus</u>
	<u>Neopanope sayi</u>
	<u>Neopanope texana</u>
	<u>Rhithrapanopeus harrissi</u>
oyster	<u>Crassostrea virginica</u>
oyster drill	<u>Urosalpinx cinerea</u>
	<u>Eupleura caudata</u>
puffer	<u>Spheroides maculatus</u>
	<u>Pseudoleuronectes americana</u>
sea star	<u>Asterias forbesi.</u>
soft shell clam	<u>Mya arenaria</u>
	<u>Panopeus herbstii</u>
tautog	<u>Tautoga onitis</u>
whelk	<u>Busycon canaliculatum</u>

LITERATURE CITED

- Abbott, R.T. 1974. American Seashells. Van Nostrand Reinhold Company, N.Y. 663 pp.
- Adamkewicz, L. 1987. Geographical effects of growth rate in the hard clam Mercenaria mercenaria. J. Shellfish Res. 7: 5 (abstract).
- Allen, J.F. 1954. The influence of bottom sediments on the distribution of five species of bivalves in the Little Annemessex River, Chesapeake Bay. Nautilus 68: 131-141.
- Anderson, W.D., W.J. Keith, F.H. Mills, M.E. Bailey, and J.L. Steinmeyer. 1978. A survey of South Carolina's hard clam resources. S.C. Wildlife and Marine Resources Department, Marine Resources Center, Tech. Rept. 32, vi + 17 p. + 15 p. appendix III.
- Andrews, 1970a. Climatic and ecological settings for growing shellfish. pp. 97-107. In Conf. on Artificial Propagation of Commercially Valuable Shellfish - Oysters. K.S. Price Jr and D. Maurer (Eds.). University Delaware Press, Newark, DE, USA.
- Andrews, 1970b. The mollusc fisheries of Chesapeake Bay (USA). pp: 847-856 In: Proc. Symposium on Mollusca, Pt. III Marine Biological Association of India. Cochin, India.
- Ansell, A.D. 1967. Egg production of Mercenaria mercenaria. Limnol. Oceanogr. 12: 172-176
- Ansell, A.D. 1968. The rate of growth of the hard clam Mercenaria mercenaria (L) throughout the geographical range. J. de Conseil. 31: 364-409.
- Arnold, W.S. 1983. The effect of prey size, predator size, and sediment composition on the rate of predation of the blue crab, Callinectes sapidus Rathbun, on the hard clam, Mercenaria mercenaria (Linne). J. Exp. Mar. Biol. Ecol. 80: 207-219.
- Barnes, R.D. 1980. Invertebrate Zoology. 4th Ed. Saunders College/Holt, Rinehart, Winston, Philadelphia, PA, USA. 1089 pp.
- Becerra-Huencho, R. M. 1984. The effect of organotin and copper sulfate on the late development and presettlement behavior of the hard clam Mercenaria mercenaria. MS Thesis, Chesapeake Biological Laboratory, University of Maryland, Solomons, Maryland. 83pp.
- Behrens, W.J. and I.W. Duedall. 1981. The behavior of heavy metals in transplanted hard clams, Mercenaria mercenaria. Int. Counc. Explor. Sea J. Cons. 39: 223-230.

- Belding, D.L. 1931. The quahaug fishery of Massachusetts. Commonwealth of Massachusetts, Department of Conservation, Division of Fish and Game, Mar. Serv. 2. 41 pp.
- Bender, M.E., W.J. Hargis, Jr., R.J. Huggett, and M.H. Roberts, Jr. 1988. Effects of polynuclear aromatic hydrocarbons on fishes and shellfishes: An overview of research in Virginia. Mar. Environ. Res. 24: 237-241.
- Blaylock, R. A. 1989. A massive school of cownose rays in the Chesapeake Bay. Copeia 1989(3): 744-748.
- Boehm, P.D. and J.G. Quinn. 1977. The persistence of chronically accumulated hydrocarbons in the hard shell clam Mercenaria mercenaria. Mar. Biol. 44: 227-233.
- Bricelj, V.M. and R.E. Malouf. 1980. Aspects of reproduction of hard clams, Mercenaria mercenaria, in Great South Bay, New York. Proc. Natl. Shellfisheries Assoc. 70: 216-229.
- Bricelj, V.M. and R.E. Malouf. 1984. Influence of algal and suspended sediment concentrations on the feeding physiology and growth of the hard clam, Mercenaria mercenaria. Mar. Biol. 84: 155-165.
- Bricelj, V.M., R.E. Malouf, and C. de Quillefeldt. 1984. Growth of juvenile Mercenaria mercenaria and the effect of resuspended bottom sediments. Mar. Biol. 84: 167-173.
- Butler, P.A. 1964. Commercial fisheries investigations. In Pesticide-Wildlife Studies, 1963. U.S. Fish Wildlife Service Circ. 199, p. 5-28.
- Butler, P.A. 1966. Pesticides in the marine environment. In. Pesticides in the Environment and their Effects on Wildlife. J. Appl. Ecol. 3 (Suppl.): 243-259.
- Butler, P.A. 1971. Influence of pesticides on marine ecosystems. Proc. Royal Soc. London, Series B, 177: 321-329.
- Butler, P.A. 1973. Organochlorine residues in estuarine mollusks, 1965-1972- National pesticide monitoring program. Pt. I. General summary and conclusions. In Residues in Fish, Wildlife, and Estuaries. Pestic. Monitor. J. 6: 238-246. Pt. II. Residue data - Individual States. Sect. C: Delaware: 263-267. Pt. III. Sect J: New York: 303-315.
- Butman, C.A., J.P. Grassle, and C.M. Webb. 1988. Substrate choices made by marine larvae settling in still water and in a flume flow. Nature 333: 771-773.

- Byrne, C.J. and J.A. Calder. 1977. Effect of the water-soluble fractions of crude, refined and waste oils on the embryonic and larval stages of the quahog clam, Mercenaria sp. Mar. Biol. 40: 225-231.
- Calabrese, A. 1972. How some pollutants affect embryos and larvae of American oyster and hard clam. Mar. Fish. Rev. 34: 66-77.
- Calabrese, A. and H.C. Davis. 1966. The pH tolerance of embryos and larvae of Mercenaria mercenaria and Crassostrea virginica. Biol. Bull. 131: 427-436.
- Calabrese, A. and D.A. Nelson. 1974. Inhibition of embryonic development of the hard clam, Mercenaria mercenaria, by heavy metals. Bull. Environm. Contam. Toxicol. 11: 92-97.
- Calabrese, A., E. Gould, and F.P. Thurberg. 1982. Effects of toxic metals in marine animals of the New York Bight: Some laboratory observations. In: Mayer, G.F. (ed.). Ecological Stress and the New York Bight: Science and Management. Estuarine Res. Fed., Columbia, N.C. p. 281-297.
- Calabrese, A., F.P. Thurberg, and E. Gould. 1977a. Effects of cadmium, mercury, and silver on marine animals. Mar. Fish. Rev. 39: 5-11.
- Calabrese, A., J.R. MacInnes, D.A. Nelson, and J.E. Miller. 1977b. Survival and growth of bivalve larvae under heavy-metal stress. Mar. Biol. 41: 179-184.
- Carriker, M.R. 1961. Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve, Mercenaria mercenaria. J. Elisha Mitchell Scientific Soc. 77: 168-241.
- Castagna, M.R., L.M. Mason, and F.C. Biggs. 1970. Hard clam culture methods developed at VIMS. Aggregates on bottom protect seed clams from predators. Va. Inst. Mar. Sci., Mar. Resour. Adv. Ser. 4, 3 p.
- Castagna M. and P. Chanley. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginian waters on the western mid-Atlantic coast. Malacologia. 12: 47-96.
- Castagna M. and J.N. Kraeuter. 1977. Mercenaria culture using stone aggregate for predator protection. Proc. Natl. Shellfisheries Assoc. 67: 1-6.
- Chanley, P.E. 1958. Survival of juvenile bivalves in water of low salinity. Proc. Natl. Shellfisheries Assoc. 48: 52-65.
- Chanley, P. and J.D. Andrews. 1971. Aids for identification of bivalve larvae of Virginia. Malacologia. 11: 45-119.

- Chestnut, A.F. 1951. Growth rates and movements of hard clams, Venus mercenaria. Proc. Gulf and Carib. Fish. Inst., 4th Ann. Sess.: 49-59.
- Courtney, W.A.M. and G.R.W. Denton. 1976. Persistence of polychlorinated biphenyls in the hard-clam (Mercenaria mercenaria) and the effect upon the distribution of these pollutants in the estuarine environment. Envir. Pollut. 10: 55-64.
- Davis, H.C. 1958. Survival and growth of clam and oyster at different salinities. Biol. Bull. 114: 296-307.
- Davis, H.C. 1960. Effects of turbidity-producing materials in sea water on eggs and larvae of the clam (Venus (Mercenaria) mercenaria). Biol. Bull. 118: 48-54.
- Davis, H.C. 1961. Effects of some pesticides on eggs and larvae of oysters (Crassostrea virginica) and clams (Mercenaria mercenaria). Comm. Fish. Rev. 23: 8-23.
- Davis, H.C. and A. Calabrese. 1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of M. mercenaria and C. virginica. U.S. Fish Wildl. Serv. Fish. Bull. 63: 643-655.
- Davis, H.C. and P.E. Chanley. 1956. Spawning and egg production of oysters and clams. Proc. Natl. Shellfisheries Assoc. 46: 40-58.
- Davis, H.C. and H. Hidu. 1969a. Effects of pesticides on embryonic development of clams and oysters and on survival and growth of the larvae. U.S. Fish Wildl. Serv. Fish. Bull. 67: 393-405.
- Davis, H.C. and H. Hidu. 1969b. Effects of turbidity-producing substances in sea water on eggs and larvae of three genera of bivalve molluscs. Veliger 11: 316-323.
- Dow, R.L. and D.E. Wallace. 1955. Natural redistribution of a quahog population. Science 122: 641-642.
- Eldridge, P.J. and A.G. Eversole. 1982. Compensatory growth and mortality of the hard clam, Mercenaria mercenaria (Linnaeus, 1758) The Veliger, 24(3): 276 - 278.
- Eisler, R. and M.P. Weinstein. 1967. Changes in metal composition of the quahog clam, Mercenaria mercenaria, after exposure to insecticides. Chesapeake Sci. 8: 253-258.
- Eisler, R., G.R. Gardner, R.J. Hennekey, G. LaRoche, D.F. Walsh, and P.P. Yevich. 1972. Acute toxicology of sodium nitrilotriacetic acid (NTA) and NTA-containing detergents to marine organisms. Water Research, 6: 1009-1027.

- Engle, R.H., M.J. Neat, and R.E. Hillman. 1972. Sublethal chronic effects of DDT and Lindane on glycolytic and gluconeogenic enzymes of the quahog, Mercenaria mercenaria. In Marine Pollution and Sea Life. M. Ruivo (ed.). Fishing News (Books) Ltd., London, p. 257-260.
- Epifanio, C.E. and R.F. Srna. 1975. Toxicity of ammonia, nitrite ion, nitrate ion, and orthophosphate to Mercenaria mercenaria and Crassostrea virginica. Mar. Biol. 33: 241-246.
- Eversole, A.G. 1987. Species Profiles: Life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)--hard clam. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.75) U.S. Army Corps of Engineers, TR EL-82-4. 33 pp.
- Eversole, A.G., L.W. Grimes, and P.J. Eldridge. 1986. variation in growth of hard clams, Mercenaria mercenaria. American Malacological Bulletin. 42: 149-155.
- Gibbons, M.C. 1984. Predation of juveniles of the hard clam, Mercenaria mercenaria (Linne) by fifteen invertebrate species with special reference to crabs. J. Shellfish Res. 4: 90 (abstract).
- Gibbons, M.C. and M. Castagna. 1985. Biological control of predation by crabs in bottom cultures of hard clams using a combination of crushed stone aggregate, toadfish, and cages. Aquaculture 40: 189-191.
- Gosner, K.L. 1978. A field guide to the Atlantic Seashore. Houghton Mifflin Company. Boston.
- Grizzle, R.E. and P.J. Morin. 1989. Effects of tidal currents, seston, and bottom sediments on growth of Mercenaria mercenaria: results of a field experiment. Mar. Biol. 102:85-93.
- Hamwi, A. 1968. Pumping rate of Mercenaria mercenaria as a function of salinity and temperature. Proc. Natl. Shellfisheries Assoc. 58: 4 (Abstract)
- Hamwi, A. 1969. Oxygen consumption and pumping rate of Mercenaria Mercenaria. Ph.D. Dissertation. Rutgers University, New Brunswick, N.J. 185 p.
- Haskin, H.H. 1955. Further growth studies on the hard clam, Venus mercenaria. Proc. Natl. Shellfisheries Assoc. 42: 181-187.
- Haven, D.S. 1970. A study of the hard and soft clam resources of Virginia. U.S. Fish Wildl. Serv., Comm. Fish. Resources Devel. Act, Final Contract Report, 69 p.

- Haven, D.S. and J.D. Andrews. 1957. Survival and growth of Venus mercenaria, Venus campechiensis, and their hybrids in suspended trays and on natural bottoms. Proc. Natl. Shellfisheries Assoc. 47: 43-49.
- Haven, D.S. and J.G. Loesch. 1973. Summary, conclusions, and Recommendations based on an investigation into the commercial aspects of the hard clam fishery and development of commercial gear for the harvest of molluscs. Final report: Commercial Fisheries Research and Development Act. Va. Inst. Mar. Sci., Gloucester Point, Virginia, 108 p.
- Haven, D.S., J.S. Loesch, and J.P. Whitcomb. 1973. An investigation into commercial aspects of the hard clam fishery and development of commercial gear for the harvest of molluscs. Final contract report for the period 1 July, 1970 through 30 June, 1973. Commercial Fisheries Research and Development Act. Va. Inst. Mar. Sci., Gloucester Point, Virginia, 112 p.
- Henderson, J.T. 1929. Lethal temperatures of Lamellibranchiata. Contr. Canad. Biol. Fish., N.S. 4: 399-411.
- Heppell, D. 1961. The naturalization in Europe of the quahog, Mercenaria mercenaria (L.). J. Conchol. 25: 21-34.
- Hidu, H. 1965. Effects of synthetic surfactants on the larvae of clams (Mercenaria mercenaria). J. Water Poll. Control Fed. 37: 262-270.
- Hobbs, C.H., R.J. Byrne, R.A. Gammisch, and R.J. Diaz. 1985. Sand for beach nourishment in lower Chesapeake Bay. pp 790 - 811 in: Proceedings of Fourth Symposium on Coastal and Ocean Management. American Soc. Civil Engineering.
- Huggett, R.J., M.M. Nichols, and M. Bender. 1980. Kepone contamination of the James River estuary. In: Baker, R.A., ed. Contaminants and sediments, vol. 1. Science Publishers, Ann Arbor, MI. p 33-52.
- Jefferies, H.P. 1964. Comparative studies on estuarine zooplankton. Limnol. Oceanogr. 9: 348-358.
- Keck, R., D. Maurer, and R. Malouf. 1974. Factors influencing the setting behavior of larval hard clams, Mercenaria mercenaria. Proc. Natl. Shellfisheries Assoc. 64: 59-67.
- Kennedy, V.S., W.H. Roosenburg, M. Castagna, and J.A. Mihursky. 1974. Mercenaria mercenaria (Mollusca: Bivalva): Temperature-time relationships for survival of embryos and larvae. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 72: 1160-1166.
- Knaub, R.S., and A.G. Eversole. 1988. Reproduction of different stocks of Mercenaria mercenaria. J. Shellfish Res. 7(3): 371-376.

- Kraeuter, J.N., M. Castagna, and R. van Dressel. 1981. Egg size and larval survival of Mercenaria mercenaria (L.) and Argopectin irradians (Lamarck). J. Exp. Mar. Biol. Ecol. 56: 3-8.
- Larsen, P.F. 1979. The distribution of heavy metals in the hard clam, Mercenaria mercenaria, in the lower Chesapeake Bay region. Estuaries. 2: 1-8.
- Lippson, A.J. (Ed.). 1973. Chesapeake Bay in Maryland - An atlas of natural resources. Natural Resources Inst. Univ. Md., Contr. 500, Johns Hopkins Press, viii + 56 p.
- Loesch, J.G. and D.S. Haven. 1973. Estimated growth functions and size-age relationships of the hard clam, Mercenaria mercenaria, in the York River, Virginia. Veliger 16: 76-81.
- Loosanoff, V. 1936. Sexual phases in the quohog. Science 83: 287-288.
- Loosanoff, V.L. 1937a. Development of the primary gonad and sexual phases in Venus mercenaria Linneaus. Biol. Bull. 72: 389-405.
- Loosanoff, V.L. 1937b. Seasonal gonadal changes of adult clams, Venus mercenaria (L.). Biol. Bull. 72: 406-416.
- Loosanoff, V.L. 1959. The size and shape of metamorphosing larvae of Venus (Mercenaria) mercenaria grown at different temperatures. Biol. Bull. 117: 308-318.
- Loosanoff, V.L. and H.C. Davis. 1963. Rearing of bivalve mollusks. Adv. Mar. Biol. F.S. Russell (ed.). Academic Press, N.Y. 1: 1-136.
- Loosanoff, V.L., H. Davis, and P. Chanley. 1953. Lack of relation between age of oysters or clams and quality of their spawn. U.S. Dept. Interior, Fish Wildl. Ser., Fish. Biol. Lab. Milford, Conn., Bull. 4, 2 p.
- Lough, G.H. 1975. A reevaluation of the combined effects of temperature and salinity on the survival and growth of bivalve larvae using response surface techniques. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 73: 86-94.
- Lutz, R.A. and D.C. Rhoads. 1980. Growth patterns within the molluscan shell-An overview. Chapt. 6 In Rhoads, D.C., and R.A. Lutz (eds) Skeletal growth of aquatic organisms - Biological records of environmental change, p 203-254. Plenum Press, NY.
- Lutz, R.A. and H.H. Haskin. 1984. Some observations on the longevity of the hard clam Mercenaria mercenaria (Linne). J. Shellfish Res. 5: 39 (Abstract).

- MacKenzie, C.L. 1977. Predation on hard clam (Mercenaria mercenaria) populations. Trans. Am. Fish. Soc. 106: 530-537.
- Malinowski, S.M. and R.B. Whitlatch. 1984. Natural survivorship of young hard clams, Mercenaria mercenaria (Linne), in eastern Long Island Sound. J. Shellfish Res. 4: 91 (abstract).
- McHugh, J.L., M.W. Sumner, P.J. Flagg, D.W. Lipton, and W.J. Behrens. 1982. Annotated bibliography of the hard clam (Mercenaria mercenaria). U.S. Dept. Commerce. NOAA Tech. Rept. NMFS SSRF-756.
- McHugh, J.L. and M.W. Sumner. 1988. Annotated bibliography II of the hard clam Mercenaria mercenaria. U.S. Dept. Commerce. NOAA Tech. Rept. NMFS 68.
- Menzel, R.W. and H.W. Sims. 1964. Experimental farming of hard clams, Mercenaria mercenaria, in Florida. Proc. Natl. Shellfish Assoc. 53: 103-109.
- Morrison, G. 1971. Dissolved oxygen requirements for embryonic and larval development of the hardshell clam, Mercenaria mercenaria. J. Fish. Res. Bd. Canada 28: 379-381.
- Olla, B.L., A.J. Bejda, and W.H. Pearson. 1983. Effects of oiled sediment on the burrowing behavior of the hard clam, Mercenaria mercenaria. Mar. Environ. Res. 8: 183-193.
- Peterson, C.H. 1986. Enhancement of Mercenaria mercenaria densities in seagrass beds: Is pattern fixed during settlement or altered by subsequent differential survival? Limnol. Oceanogr. 31: 200-205.
- Pratt, D.M. 1953. Abundance and growth of Venus mercenaria and Callocardia morrhuana in relation to the character of bottom sediments. J. Mar. Res. 12: 60-74.
- Pratt, D.M. and D.A. Cambell. 1956. Environmental factors affecting growth in Venus mercenaria. Limnol. Oceanogr. 1:2-17.
- Pringle, B.H., D.E. Hissong, E.L. Katz, and S.T. Mulawka. 1968. Trace metal accumulation by marine molluscs. J. Sanit. Eng. Div., Proc. Am. Soc. Civil Eng. Proceed. Pap. 5970 (Sa 3): 455-475.
- Quayle, D.B. and N. Bourne. 1972. The clam fisheries of British Columbia. Fish. Res. Board Can. Bull. 179. 70pp.
- Rice, T.R. and R.J. Smith. 1958. Filtering rates of the hard clam (Venus mercenaria) determined with radioactive plankton. U.S. Fish Wildl. Serv. Fish. Bull. 58: 73-82.

- Roberts, M.H., Jr. 1987. Acute toxicity of tributyltin chloride to embryos and larvae of two bivalve molluscs, Crassostrea virginica and Mercenaria mercenaria. Bull. Environ. Contam. Toxicol. 39: 1012-1019.
- Roberts, M.H., Jr., R.J. Diaz, M.E. Bender, and R.J. Huggett. 1975. Acute toxicity of chlorine to selected estuarine species. J. Fish. Res. Bd. Canada 32: 2525-2528.
- Romeril, M.G. 1979. The occurrence of copper, iron and zinc in the hard shell clam, Mercenaria mercenaria, and sediments of Southampton Water. Estuarine Coastal Mar. Sci. 9: 423-434.
- Savage, N.B. 1976. Burrowing activity in Mercenaria mercenaria (a (L.) and Spisula solidissima (Dillwyn) as a function of temperature and dissolved oxygen. Mar. Behav. Physiol. 3: 221-234.
- Scott, G.I. and W.B. Vernberg. 1979. Seasonal effects of chlorine produced oxidants on the growth, survival and physiology of the American oyster, Crassostrea virginica (Gmelin). In: Marine Pollution: Functional Responses. W.B. Vernberg, F.P. Thurberg, A. Calabrese, and F.J. Vernberg (eds.). Academic Press, New York: 415-435.
- Shelton, R.G.J. 1971. Two recent problems in oil pollution research. Internat. Council Expl. Sea, Fish. Improvement Comm., Copenhagen, 9 p.
- Shuster, C.N., Jr. and B.H. Pringle. 1968. Effects of trace metals on estuarine mollusks. Proc. 1rst Mid-Atlantic Industrial Waste Conf., Univ. Delaware, CE-5: 285-304.
- Sindermann, C.J. and A. Rosenfield. 1967. Principal diseases of commercially important bivalve Mollusca and Crustacea. U.S. Fish Wildl. Serv. Fish. Bull. 66: 335-385.
- Stanley, J.G. 1985. Species Profiles: life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic)--hard clam. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.41) U.S. Army Corps of Engineers, TR EL-82-4. 24 pp.
- Stanley, J.G. and R. Dewitt. 1983. Species Profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)--hard clam. U.S. Fish Wildl. Serv. FWS/OBS-82?11/18. U.S. Army Corps of Engineers, TR EL-82-4. 19 pp.
- Stewart, J.E. 1974. Potential for culture of invertebrates in Canada. In Aquaculture in Canada. The practice and the promise. H.R. MacCrimmon, J.E. Stewart, and J.B. Brett. Bull. Fish. Res. Bd. Canada 188: 35-52.
- Taxiarchis, L.N. 1955. Observations concerning predation on Venus at Morgan's Bay, Surry, Maine, 1954. 5th Conf. on Clam Research, U.S. Dept. Interior, Bu. Comm. Fish., 1 p. (mimeo).

- Tenore, K.R. and W.N. Dunstan. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.* 21: 190-195.
- Tenore, K.R., J.C. Goldman, and J.P. Clarner. 1973. The food chain dynamics of the oyster, clam, and mussel in an aquaculture food chain. *J. Exp. Mar. Biol. Ecol.* 12: 157-165.
- Thurberg, F.P., A. Calabrese, and M. A. Dawson. 1974. Effects of silver on oxygen consumption of bivalves at various salinities. *In* *Pollution and Physiology of Marine Organisms*. Academic Press Inc., New York: 67-78.
- Van Winkle, W., S.Y. Feng, and H.H. Haskin. 1976. Effect of temperature and salinity on the extension of siphons by *Mercenaria mercenaria*. *J. Fish. Res. Board Can.* 33: 1540-1546.
- Walne, P.R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. Mar. Biol. Assoc. U.K.* 52: 345-372.
- Wells, H.W. 1957. Abundance of the hard clam *Mercenaria mercenaria* in relation to environmental factors. *Ecology*. 38: 123-128.
- Whetstone, J.M. and A.E. Eversole. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. *Proc. Natl. Shellfisheries Assoc.* 68: 42-48.
- Wood, L. and W.J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. In Crisp, D.J., ed., *Fourth Marine Biology Symposium*, Cambridge University Press. 29-44.
- Woodwell, G.M., C.F. Wurster, Jr., and P.A. Isaacson. 1967. DDT residues in an East Coast Estuary: A case of biological concentration of a persistent insecticide. *Science* 156: 821-823.

