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## EFFECTS OF INTENSIVE FISHING EFFORT ON THE POPULATION STRUCTURE OF QUAHOGS, *MERCENARIA MERCENARIA* (LINNAEUS 1758), IN NARRAGANSETT BAY\*

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**ABSTRACT** Quahogs, *Mercenaria mercenaria*, and sediment samples were collected from three locations in Narragansett Bay: Greenwich Cove, Greenwich Bay, and the West Passage of Narragansett Bay. Greenwich Cove has been closed to shellfishing for several decades. The average density of quahogs in the cove was 190/m<sup>2</sup>, ranging from 32 m<sup>2</sup>-500/m<sup>2</sup> in 30 quadrats. The average valve length of quahogs in Greenwich Cove was 62 mm. Adjacent to Greenwich Cove in Greenwich Bay which has been heavily fished since the 1930s. The average density of quahogs in Greenwich Bay was 78/m<sup>2</sup>, ranging from 8/m<sup>2</sup>-184/m<sup>2</sup>. The average valve length was 31 mm. There were no significant differences in salinity, Secchi disk turbidity or total organic content of sediments between these two sites. There was a slightly higher content of very fine-grained sands (<125 µm), silts, and clays in the Greenwich Cove sediments. The average *Mercenaria* density at another closed site on the West Passage of Narragansett Bay was 46/m<sup>2</sup> with an average valve length of 61 mm. The lower density may be due to higher silt and clay content of the sediments. There were significantly more juvenile (<40 mm) quahogs in the heavily fished area ( $p < 0.01$ , ANOVA). Determination of age by shell growth rings showed that quahogs in the bay were 12 years of age or less. Ages were greater in the closed areas and exceeded 25 years in the largest individuals. Growth data from quahogs in the closed areas was fit to the von Bertalanffy growth equation. This yielded asymptotic valve length maxima ( $L_{max}$ ) of 110 mm  $\pm$  9.6 (SE) in the West Passage and 86 mm  $\pm$  4.7 (SE) in the cove, suggesting density-dependent stunting in the latter site. Active fishing tends to remove adults from the population and enhance either the set or survival of juvenile quahogs. The mechanism for increasing the juvenile density is not understood; possible explanations include removal of competing adults and sediment disturbance/turnover as a result of the fishing methods. Reburrowing of quahogs placed on the sediment surface was studied. Results indicate that the largest adults (>86 mm valve length) have the least ability to reburrow.

**KEY WORDS:** *Mercenaria*, population structure, Narragansett Bay, shellfishery, fishing effort

### INTRODUCTION

Several studies in Narragansett Bay have focused on populations of the northern quahog, *Mercenaria mercenaria* (Linnaeus 1758). Many of these studies have correlated bottom type with clam abundance (Pratt 1953, Pratt and Campbell 1956, Saila et al. 1967). Another study has elucidated the infaunal community structure by correlating clam populations with the distribution of other infaunal species (Stickney and Stringer 1957). Other studies have been undertaken to assess the standing stock of adult clams with the aim of developing a database to aid the management of the *Mercenaria* fishery (Kovach 1968, Kovach et al. 1968, Sisson 1976).

In all of the aforementioned studies, *Mercenaria* and/or sediments were sampled by using either clam rakes or tongs, or a grab sampler from a boat. Clam tongs or rakes will not effectively sample *Mercenaria* less than about 30 mm in

valve length which escape through the teeth of the sampling device (Kovach 1968). A "clam shell" grab sampler has been used for other studies (Stickney and Stringer 1957, Saila et al. 1967). Quantitative grab sampling may possibly retain juvenile *Mercenaria*, however data on the size of individual clams were not reported.

In more recent study, Walker and Tenore (1984) sampled intertidal areas in Wassaw Sound, Georgia, by placing 1.0 m<sup>2</sup> quadrats intertidally during low tide and sieving the contents of the quadrats through a 1.0 mm mesh screen. They reported the size and numbers of *Mercenaria* to assess modestly exploited stocks with the aim of expanding the quahog fishery.

Unlike areas in the South, the quahog fishery in Narragansett Bay had begun early in this century and was well established by 1928. At that time, Greenwich Bay was one of the major areas of quahog production in Rhode Island due to its shallow waters. Only 8% of Greenwich Bay is deeper than 13 feet, making the quahog stocks well within reach of tongs (Pratt 1988). Greenwich Bay remains one of the most heavily exploited quahog grounds in Narragansett Bay (Campbell 1961; Ganz 1987). Greenwich Cove, adja-

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cent to Greenwich Bay, has been closed to shellfishing since the 1930s (J. Migliore, RI Department of Environmental Management; J. Martin, EPA Narragansett Bay Project, pers. comm.). With an area long-closed to shellfishing in such close proximity to heavily exploited beds, changes in the populations of *Mercenaria* due to fishing pressure may be readily studied by comparing the two areas.

Concomitant with a well developed fishery, efforts have been taken by management agencies to enhance the quahog fishery, especially in areas with intense fishing pressure. A state sponsored program to transplant quahogs from beds closed to shellfishing to actively fished areas has been carried out intermittently in Narragansett Bay since the 1950s (Ganz 1987, Pratt 1988). Typically, large adult quahogs are removed from dense assemblages in closed areas and moved to areas with certified clean waters. The transplanted quahogs remain undisturbed for at least 3 months before the transplant area is opened for fishing. Although this program has been carried out for several years and has the popular support of fishermen, little has been done to investigate the survival of quahogs during the transplant process.

This study aims to compare the population structure of quahogs in two areas closed to shellfishing with an area which is heavily fished. The ability of quahogs to reburrow is studied, because it is considered a key factor to the survival of transplanted quahogs.

#### MATERIALS AND METHODS

The main study area was in the Greenwich Cove area in the northwest quadrant of Narragansett Bay (Fig. 1). Greenwich Cove has been closed to shellfishing because of the presence of a sewage treatment plant and several marinas. The pollution closure line runs between Chepewanoxet Point and Long Point which form the mouth of the Cove, providing easy landmarks for enforcement purposes. The actual study site is 2 km from the sewage treatment plant outfall and 300 meters away from boat moorings. East of the pollution closure line is Greenwich Bay which is considered one of the most productive commercial and recreational shellfishing areas in Rhode Island (Ganz 1987). Tidal currents at the mouth of Greenwich Cove are semi-diurnal with a maximum velocity of approximately 0.5 m/s (Spaulding and Swanson 1984). The Greenwich Bay site is approximately 100 m east of the pollution closure line and 200 m east of the Greenwich Cove site. The Greenwich Cove and Greenwich Bay sites have been the location of a recent in-depth study of tidal exchange and nutrient loading (Dettmann et al. 1989). A secondary study area was chosen on the West Passage of Narragansett Bay adjacent to the University of Rhode Island Narragansett Bay Campus (Fig. 1). This area has been closed to shellfishing for two decades because of a small sewage treatment plant one km to the south and a nearby experimental nuclear reactor.

Thermal effluents by the reactor are negligible because of its small power output. Due to its location in the open bay, this site is subject to greater tidal current velocities than the relatively enclosed Greenwich Cove area. Maximum current velocities at the West Passage site are approximately 2.5 m/s (Spaulding and Swanson 1984).

Salinity and turbidity measurements were taken on a weekly basis in each of the sites by a hand-held refractometer and a 25 cm diameter Secchi disk. Sediment samples from each of the study sites were taken by SCUBA divers using short core tubes. The sediment cores were approximately 10 cm deep. Sediment was analyzed according to Folk's methods (1968). To determine grain size, sediment samples were dried overnight at 100°C and passed through a standard series of six sieves, beginning with a 2 mm mesh (-1.0 phi) with sequential halving to a final sieve of 62.5 µm mesh (+4.0 phi). The retained sediments on each of the sieves were weighed and expressed as a percentage of the total sediment dry weight. The sediment fraction passing through the final 62.5 µm mesh sieve was treated similarly. The total organic content (TOC) of the sediments was determined by weight loss after ignition at 550°C (Gross, 1972).

Samples of *Mercenaria* were taken from 0.25 m<sup>2</sup> quadrats placed by SCUBA diver at each of the three sites. In Greenwich Bay and Greenwich Cove, the quadrats were placed in a haphazard fashion approximately 100 m east or west of the pollution closure line in 3-5 m of water. The 100 m distance was chosen well within or well outside the pollution closure area to minimize the possibility of sampling an area which might have occasional errant commercial harvesting. At the West Passage site, quadrats were placed haphazardly along the 7-meter depth contour as determined by diver depth gauges. The upper 10 cm sediment content of the quadrat was removed by a small garden trowel and placed in a nylon mesh bag constructed with 5 mm octagonal meshes. While underwater, the mesh bag was shaken to allow sediments to filter out. It was assumed that quahogs greater or equal to 5 mm in valve length stayed in the mesh bag. The retained contents of the mesh bag were then transferred to polyethylene bags for transport and live storage pending sorting in the laboratory. The anterior-posterior valve lengths of all collected quahogs were measured by vernier calipers. Some quahogs were set aside for other morphometric analyses. The relationships between valve length, hinge width, and shell-free wet weight of fresh blotted tissue were determined. Age of selected quahogs was estimated by counting growth rings deposited on the exterior of the shell along the edge of the hinge plate, adjacent to the ligament. It was assumed that each major ring corresponded to the annual cessation of growth at the onset of winter. The counting of external rings was verified by cutting and polishing a small subsample of shells from umbo to ventral edge and counting major dark bands in the prismatic layer corresponding to the winter

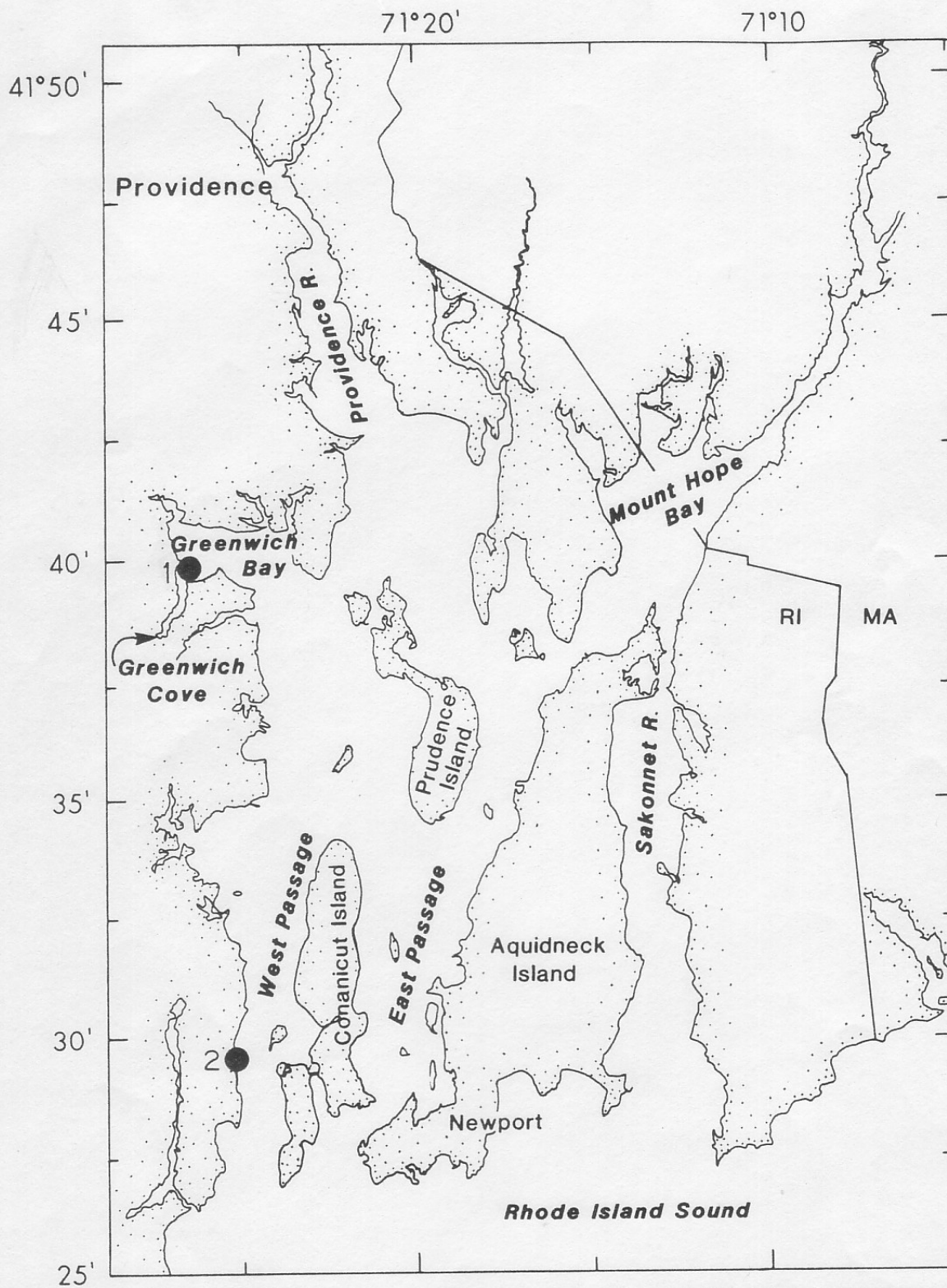


Figure 1. Narragansett Bay, Rhode Island. The study locations are on the western shore of the Bay. Location number 1 is at the mouth of Greenwich Cove, a narrow inlet off Greenwich Bay. Location number 2 is at South Ferry, on the West Passage of Narragansett Bay.

break in growth (Grizzle and Lutz 1988). Reliable age estimates of quahogs older than 15–20 years were possible only by sectioning the shell because of the close proximity of successive growth lines at the ventral edge.

Individual quadrat data were tabulated and analyzed by a microcomputer spreadsheet program (Lotus 123). Statistics and calculations using pooled data from individual sites were analyzed using the Fishery Science Application System (FSAS) (Saila et al., 1988). Subroutines of FSAS used for this study include univariate statistics, length-frequency analysis and non-linear least squares regression for curve fitting of the von Bertalanffy growth equation.

To determine the reburrowing of harvested quahogs, three subsets of quahogs ranging from 25–100 mm in valve length were selected. The shells of the quahogs were washed in fresh water, allowed to air dry, and painted with yellow enamel spray paint for easy underwater identification. Divers then returned the quahogs to their collection site, placing them on the surface of the sediments. An iron bar was inserted to project from the sediments at the center of the pile of painted quahogs, serving as a fixed reference point. After one week, the painted quahogs were retrieved from the surface or excavated from the sediments.

## RESULTS

Measurements of salinity of surface waters and Secchi disk turbidity were taken on a weekly basis from May to July, 1989. The mean salinity in Greenwich Cove and Greenwich Bay was 27 ppt (23–30 ppt range). Secchi depths at the two sites averaged 1.8 m (1.5–2.5 m range). There were no differences in the individual daily salinity and turbidity measurements between the cove and the bay. Mean salinity and Secchi depths at the West Passage site were 29.5 ppt (28–32 ppt range) and 2.5 m (1.5–4 m range).

The sediments collected at the Greenwich Cove and Greenwich Bay sites have a similar composition (Table 1). At both locations, the sediments are sandy in character with

minor silt/clay and gravel components. There are, however, significant differences in some of the grain size fractions. The actively fished area (Greenwich Bay) has comparatively more medium to fine sands and significantly less very fine sand, silts, and clays ( $p < 0.05$ ; ANOVA). The sediments collected at the West Passage site have a significantly higher percentage of shell fragments indicated by higher percentages in the 2.0 mm and 1.0 mm gravel and coarse sand fractions. The West Passage samples also contain considerably more silts and clays as indicated by a higher percentage in the  $<63 \mu\text{m}$  fraction. The mean percentage of TOC in Greenwich Cove and Greenwich Bay sediments was  $2.53 \pm 1.09$  (SD;  $n = 9$ ) and  $2.93 \pm 1.90$ , respectively. These values, likewise, are not significantly different ( $p > 0.1$ ; ANOVA). The TOC of sediments collected at the West Passage site was  $3.91 \pm 0.52$  (SD;  $n = 9$ ) percent which is significantly higher ( $p < 0.05$ ; ANOVA) than either of the Greenwich sites.

In Greenwich Cove (Fig. 2A), a total of 1426 quahogs was collected from 30 quadrats. This corresponds to an average quahog density of 190  $\text{m}^2$ . The mean and median size of quahogs was 62 mm and 63 mm, respectively. The distribution is unimodal with the mode in the 61–63 mm size class. The number of quahogs per quadrat in Greenwich Cove was highly variable, indicating patchiness of distribution. The mean number of quahogs per quadrat was  $47.6 \pm 39.4$  (SD), ranging from 8–125 per quadrat. In adjacent Greenwich Bay (Fig. 2B), 578 quahogs were collected in 30 quadrats. This corresponds to an average density of 78/ $\text{m}^2$ . The mean and median size of quahogs was 31 mm and 30 mm, respectively. The size distribution is polymodal with a majority of the quahogs less than 50 mm in valve length. The mean number of quahogs per quadrat was  $19.4 \pm 10.1$  (SD), ranging from 2–46. In comparing the size distribution of quahogs in Greenwich Cove and Greenwich Bay, there are significantly higher numbers ( $p < 0.01$ ) of juvenile quahogs ( $<40$  mm valve length) in Greenwich Bay. There is no significant difference in the

TABLE 1.

Sediment samples from the pollution closure area and the fished area were dried and sieved. Units are percent of total sample weight. Significant differences between sediment fractions in the open and closed area were determined by one-way analysis of variance and Fischer's least significant difference test. All values except for those indicated by an asterisk (\*) are significantly different ( $p < 0.05$ ; ANOVA) from sediments in closed area of Greenwich Cove.

Mesh Size	(Phi)	Greenwich Cove Closed Area (mean $\pm$ SD) (n = 9)	Greenwich Bay Open Area (mean $\pm$ SD) (n = 9)	West Passage Closed Area (mean $\pm$ SD) (n = 9)
2.0 mm	(-1.0)	3.60 $\pm$ 1.23	0.76 $\pm$ 0.47	13.18 $\pm$ 4.35
1.0 mm	(0.0)	1.68 $\pm$ 0.39	1.26 $\pm$ 0.56*	7.23 $\pm$ 2.27
500 $\mu\text{m}$	(+1.0)	3.89 $\pm$ 0.71	3.94 $\pm$ 1.95*	8.40 $\pm$ 3.24
250 $\mu\text{m}$	(+2.0)	19.55 $\pm$ 2.76	24.63 $\pm$ 3.52	19.39 $\pm$ 4.71*
125 $\mu\text{m}$	(+3.0)	40.50 $\pm$ 3.16	49.26 $\pm$ 4.13	32.32 $\pm$ 8.50
63 $\mu\text{m}$	(+4.0)	28.29 $\pm$ 2.72	19.07 $\pm$ 2.71	9.76 $\pm$ 1.05
<63 $\mu\text{m}$	(<4.0)	2.47 $\pm$ 0.61	1.06 $\pm$ 0.28	9.68 $\pm$ 2.32

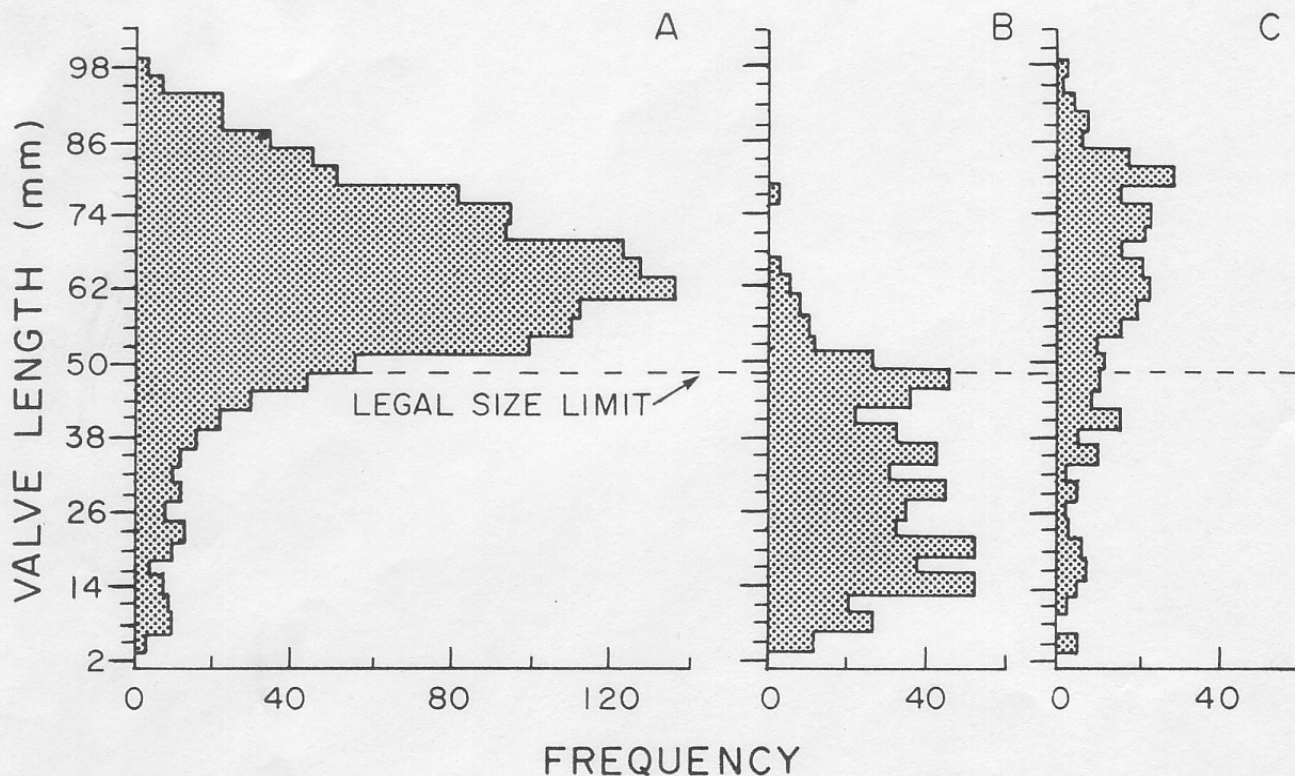


Figure 2A-C. Quahogs, *Mercenaria mercenaria*, were collected by SCUBA divers from 30 quadrats (0.25 m<sup>2</sup>) in each of three sites in Narragansett Bay. The sites are: (A) Greenwich Cove, (B) Greenwich Bay, and (C) South Ferry, West Passage. Histograms represent total numbers of quahogs in size classes of 3 mm increments. The indicated valve lengths are the size class midpoints. The dashed line represents the Rhode Island legal size limit for quahogs which is a one-inch hinge width, which corresponds approximately to a valve length of 48 mm.

numbers of quahogs in the 40–48 mm size classes between the two sites. This suggests that there may be general compliance among fishermen to the laws prohibiting the harvest of undersized shellfish. The lowest densities of quahogs were found at the West Passage site (Fig. 2C). A total of 344 quahogs was collected in 30 quadrats, representing an average density of 46/m<sup>2</sup>. The mean and median size of quahogs at the West Passage site was 61 mm and 64 mm, respectively, with the major mode in the 79–81 mm size class. The distribution of quahogs in the West Passage is also patchy with an average  $11.5 \pm 6.4$  (SD) per quadrat, ranging from 0–25 per quadrat.

Quahogs of varying size from each of the three sites were selected for age estimation. The maximum age and corresponding size of the quahogs were 33 years and 111 mm from West Passage; 34 years and 87 mm from Greenwich Cove; and 12 years and 74 mm in Greenwich Bay. The relation between size and estimated age of quahogs at each of the sites was plotted (Fig. 3). The data from Greenwich Cove and the West Passage Site were fit to the von Bertalanffy growth equation:

$$L_{(t)} = L_{\max}(1 - e^{-K(t-t_0)}) \quad (1)$$

where  $L_{(t)}$  is length at time in years ( $t$ );  $L_{\max}$  is the maximum theoretical valve length;  $t_0$  is time zero; and  $K$  is an empirically determined growth constant. Estimates for  $L_{\max}$

and  $K$  with West Passage quahogs were  $110 \text{ mm} \pm 9.6$  (SE) and  $8.7 \times 10^{-2} \pm 2.9 \times 10^{-2}$  (SE) respectively. The  $L_{\max}$  and  $K$  estimates for Greenwich Cove quahogs were  $86 \text{ mm} \pm 4.7$  (SE) and  $1.0 \times 10^{-1} \pm 2.8 \times 10^{-2}$  (SE). One criterion of the goodness of fit of the von Bertalanffy growth curve to the data is the estimated value of  $t_0$ . In both cases of data from West Passage and Greenwich Cove, the abscissa origin of the data plot falls within one standard error of the estimated value of  $t_0$ . The estimated von Bertalanffy growth parameters for quahogs collected in Greenwich Bay are not reported because insufficient numbers of large quahogs were able to be collected to give a confident estimate of  $L_{\max}$  (Knight, 1968). The largest quahog from Greenwich Bay to be aged was 77 mm in valve length and 10 years old.

In Rhode Island, as well as other states, one-inch hinge width has been established as the legally harvestable size for *Mercenaria*. To compare our data readily with the legal harvestable size limits of quahogs, we determined the relationship between valve length and hinge width (Fig. 4). These linear measurements correlate directly with a correlation coefficient ( $r$ ) of 0.988. From this regression, valve length is 1.78 times the hinge width.

The relationship between the valve length and the shell-free wet weight of *Mercenaria* tissues can be described by the allometric equation:

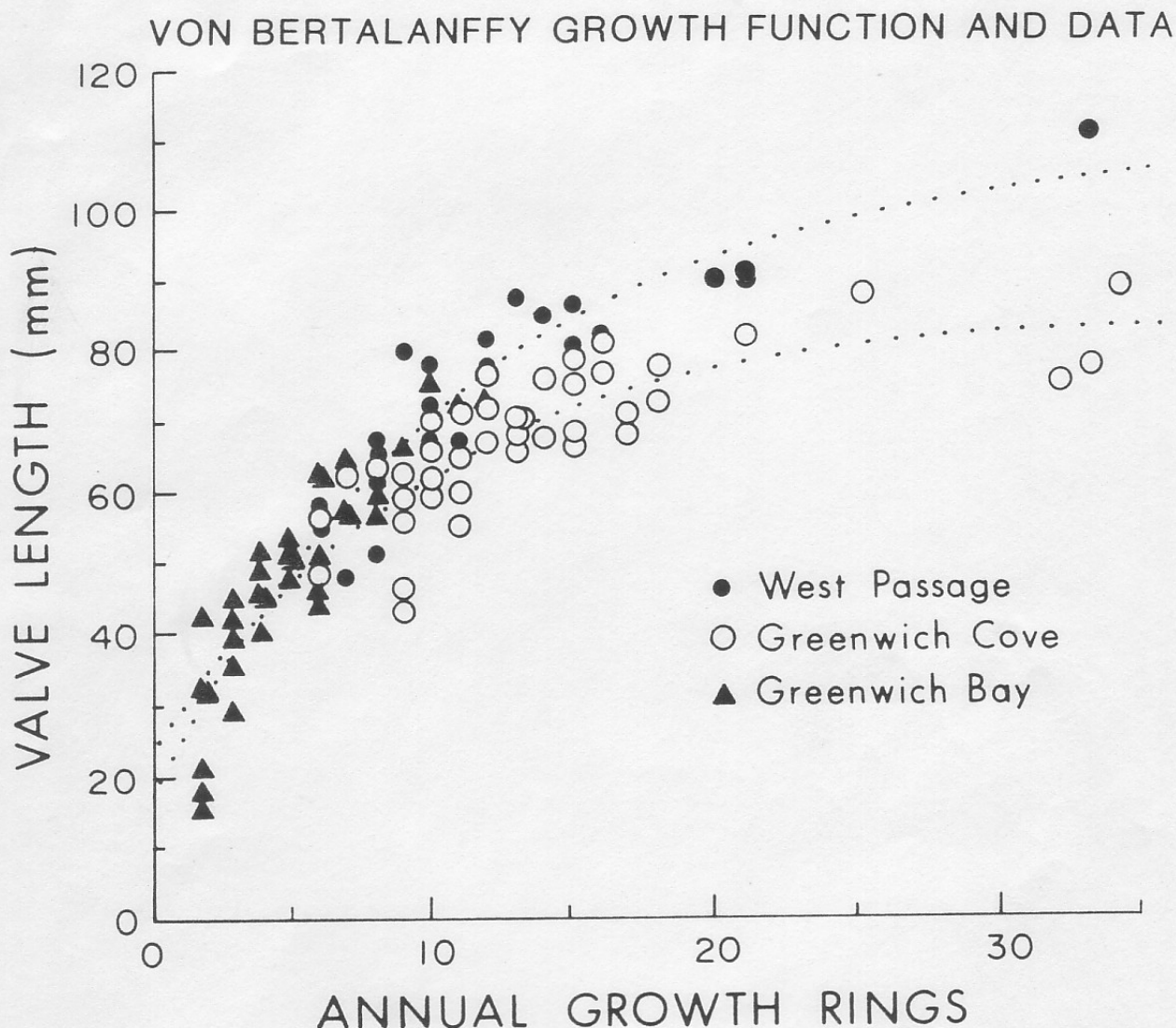


Figure 3. The valve length of quahogs from the three study sites are plotted as a function of estimated age. Von Bertalanffy growth curves were fit to Greenwich Cove and West Passage data. The  $L_{max}$  asymptotic values are 110 mm for West Passage quahogs and 86 mm for Greenwich Cove quahogs. Refer to the text for discussion of other von Bertalanffy parameters.

$$W = aL^b \quad (2)$$

where  $W$  = weight in g;  $L$  = valve length in mm; and  $a$  and  $b$  are allometric coefficients. The allometric equation can be transformed to the linear form:

$$\log W = b \log L + \log a \quad (3)$$

This transformation was used to estimate the allometric coefficients by linear regression (Fig. 5). The allometric coefficients are:  $a = 9.51 \times 10^{-5}$  and  $b = 2.81$ .

A total of 21 quahogs was recovered from the sediment surface, representing an average recovery of  $6.82\% \pm 1.11$  (SD,  $n = 3$ ). The average size of the quahogs on the surface was  $90.2 \text{ mm} \pm 4.5$  (SD,  $n = 21$ ). The minimum valve length of the quahogs on the sediment surface was 83 mm. The recovery of quahogs from the sediment surface

can be expressed as a percentage of the released quahogs which were  $\geq 86$  mm in valve length. This percentage is 18/33 or 54.5%. All but three of the 310 released quahogs were recovered from the surface or by removal from the sediment.

#### DISCUSSION

Horizontal seston fluxes, the product of phytoplankton concentration and current speed, are known to affect the growth of *Mercenaria* (Grizzle and Lutz 1989). Our Secchi depth measurements show that there is no significant difference in turbidity between the Greenwich Cove and Greenwich Bay sites. This indirectly suggests that there is no difference in phytoplankton concentration between the two sites. Recently summer and winter fluorescent dye

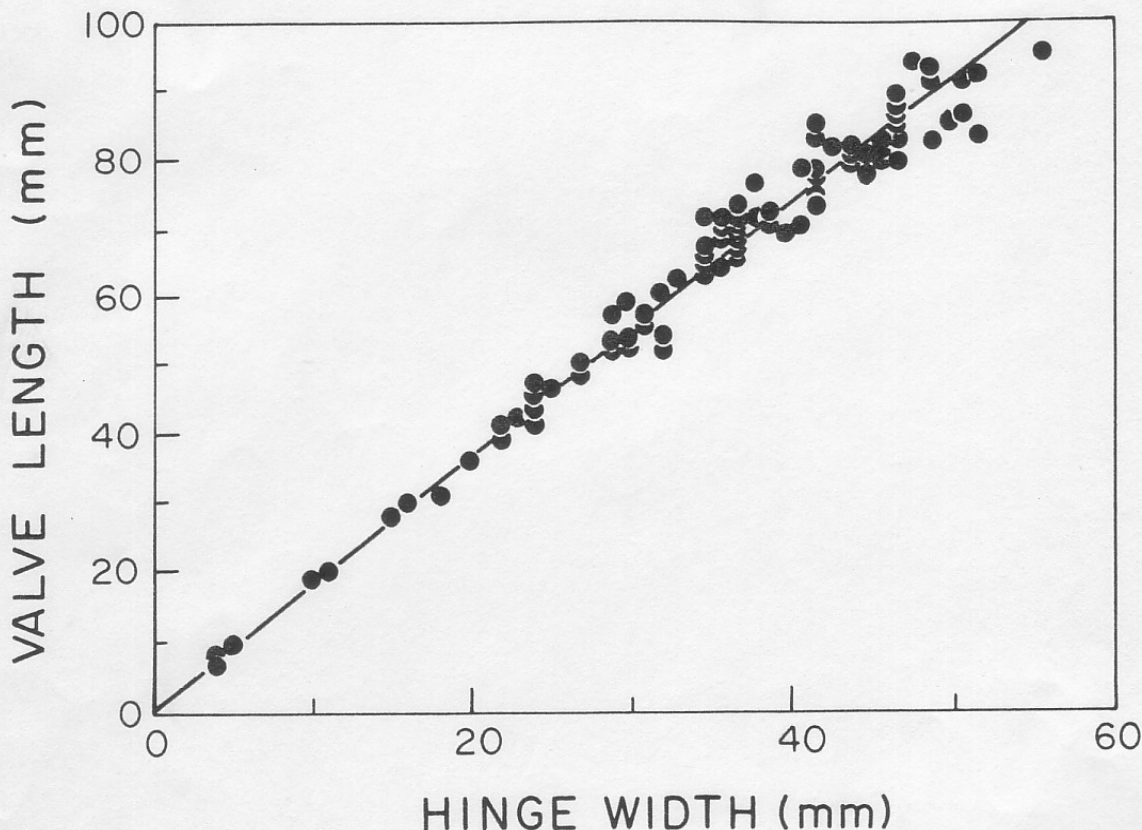


Figure 4. The value length and hinge width of *Mercenaria mercenaria* are linearly correlated ( $r = 0.988$ ;  $n = 104$ ). The calculated regression line has a positive slope of 1.78 and an intercept of 0. Quahogs were collected at the West Passage site and ranged from 7–95 mm in valve length.

surveys were conducted in Greenwich Cove with the aim of studying flushing rates of the cove and nutrient loading by the sewage treatment plant (Dettmann et al. 1989). In both surveys, dye was added to the cove waters at a continuous rate through three tidal cycles, which was sufficient for the dye to reach steady-state concentrations throughout the cove and the adjacent waters of Greenwich Bay. Sampling transects crossed the areas which we collected quahogs for this study. The data indicated no significant difference in steady-state dye concentrations between our Greenwich Cove and Greenwich Bay study sites. From this we can conclude that differences in seston fluxes or nutrient loading is not a likely explanation for the observed differences in quahog populations between the two sites. Likewise, salinity does not appear to be a factor which could explain differences in quahog populations between the two sites. Elevated total organic carbon (TOC) in sediments has been considered an indication of sewage pollution (Gross 1972). The data show that TOC in Greenwich Cove and Greenwich Bay are the same, which supports our assertion that pollutant levels from the nearby sewage treatment plant are not a factor in the distribution of quahogs. It is unlikely that the slight difference in the sediment grain size between the open and closed area can account for the gross differences in quahog densities (Table 1). Previous studies sug-

gest that quahog densities increase as the percentage of silts and clays in the sediments decreases (Pratt 1953, Pratt and Campbell 1956, Saila et al. 1967). In this study, there is much less biomass of mature *Mercenaria* in the sandier sediments. Thus the difference between quahog densities in the open and closed sites in the Greenwich Cove area probably results from differences in fishing effort.

Comparisons can be made between populations of quahogs in the two closed sites. The unimodality of the size-frequency distribution of quahogs from Greenwich Cove prevents the direct identification of any distinct year classes (Fig. 2). Although the size-frequency distribution of quahogs from West Passage exhibits some polymodality, it is not likely that this represents individual year classes. Our age-length data (Fig. 3) show considerable variability in size at any given age. This variability would be expected to obfuscate identification of individual year classes of quahogs.

Physically, quahogs collected from Greenwich Cove tended to be more blunted. The modal size of quahogs in the West Passage is 83 mm; in Greenwich Cove, 62 mm (Fig. 2). The data (Fig. 3) show that the estimated ages of quahogs in the two sites are similar. The observation of higher asymptotic growth maxima of West Passage quahogs in comparison to Greenwich Cove quahogs may



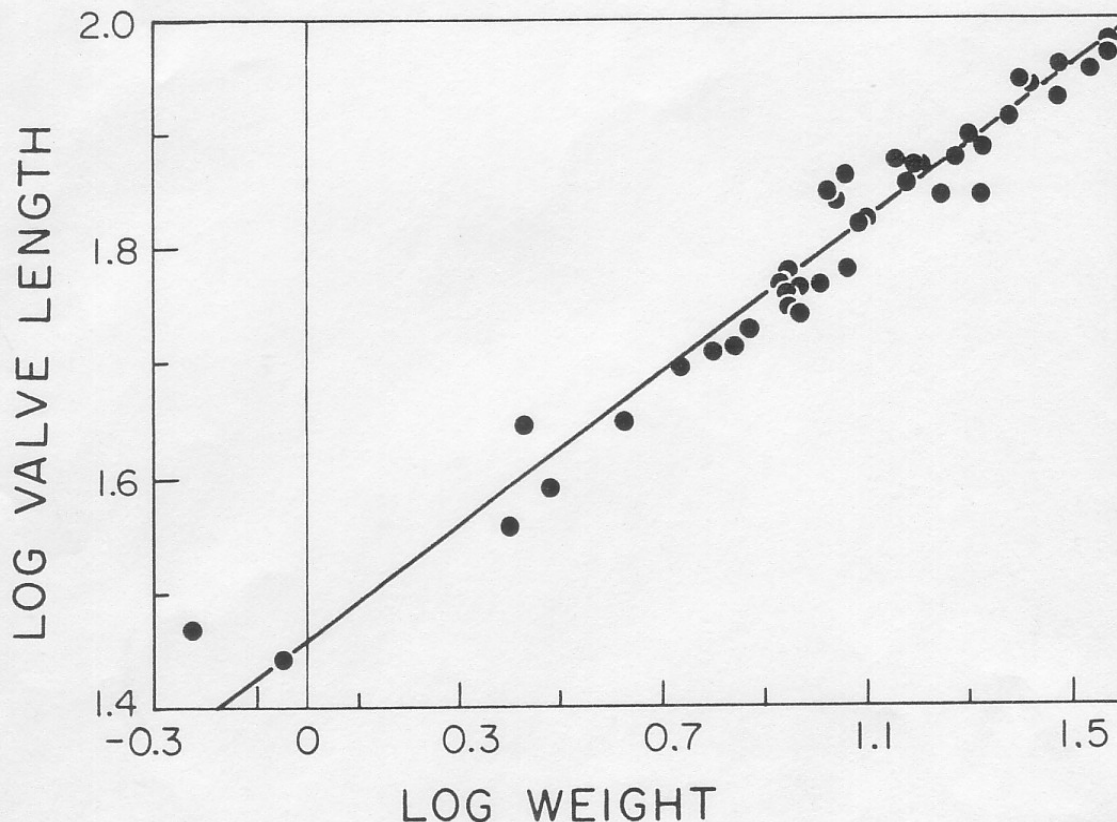


Figure 5. The valve length and shell-free tissue wet weight of *Mercenaria* can be correlated by using a linear transformation of the allometric equation. The correlation coefficient ( $r$ ) is 0.973 with a sample size ( $n$ ) of 40. Quahogs were collected at the West Passage site and ranged from 26–95 mm in valve length. Refer to text for discussion of regression coefficients.

suggest density-dependent stunting in the latter. The average density of 190/m<sup>2</sup> and the maximum density of 500/m<sup>2</sup> in Greenwich Cove are quite high. These densities of *Mercenaria* appear to be quite rare in nature and are more characteristic of densities of quahogs in intensive mariculture. Castagna (1984) suggests that field grow-out of hatchery-reared juvenile quahogs should be at densities of 250–1000/m<sup>2</sup> depending on the site. *Mercenaria* at higher densities exhibited stunting characterized by blunt valve margins and slower growth. The biomass of 1000 seed quahogs with valve lengths of 20 mm would have a total shell-free wet weight of 440 g (Fig. 5). The comparable biomass of 190 quahogs in Greenwich Cove with an average valve length of 62 mm would be 2000 g. Thus the natural standing crop biomass of quahogs in Greenwich Cove greatly exceeds the recommended stocking densities for mariculture. Natural populations of mussels *Mytilus edulis* are known to exhibit density-dependent stunting (Ricketts et al. 1968). The infaunal bivalves *Protothaca staminea* and *Chione undatella* have been shown to have depressed growth rates at high densities (Peterson 1982), as did *Anadara granosa* (Broom 1982), *Anomalocardia squamosus* and *Circe lenticularis* (Peterson & Black 1987). Peterson et al. (1985) postulated that *Mercenaria mercenaria* maintained at 80/m<sup>2</sup> (artificially high for their study area)

exhibited stunting as evidenced by a lowered rate of deposition of new shell at the ventral edge.

A number of studies have been conducted to investigate the effects of large suspension-feeding bivalves on the settlement of larvae (Hunt et al. 1987, Ertman and Jumars 1988, Black and Peterson 1988). These studies have focused upon the manipulation of densities of large adults in small (0.1 m<sup>2</sup>–1.0 m<sup>2</sup>) plots. The conclusion of all of these studies was that there was no localized inhibition of larval settlement by the presence of adult suspension-feeders in the plots. These studies however do not exclude the possibility of the inhibition of larval settlement by dense beds of adult suspension-feeding bivalves on a large scale. No large scale manipulation experiments similar to the aforementioned small scale studies have been conducted. By using a correlative analysis approach, inferences as to inhibition of larval settlement and survival by adult populations can be made. Using this approach, Hancock (1973) showed that dense infaunal assemblages of the cockle *Cardium edule* inhibited settlement of juveniles.

The data show that there are significantly higher numbers of juvenile *Mercenaria* ( $p < 0.01$ , ANOVA) in the area open to fishing than in either of the two closed areas. There are a number of possible explanations for this observation. The first explanation relates to the large scale

removal of the adult quahogs. Woodin (1976) and Williams (1980) found that the survival of larval and post-set juveniles of various bivalve mollusks or other infaunal invertebrates is enhanced when there are lower densities of adults. At high densities of filter-feeding adults, there is the potential for larval loss through larviphagy and less available space for settlement and growth. More recent work (Butman 1986) suggests that hydrodynamic factors such as ex-current siphonal currents of dense assemblages of bivalves may act to prevent larval settlement. Meadows and Campbell (1972) concluded that the presence of some adult infaunal invertebrates may provide various chemical cues which promote settlement of the larval forms. More recent work has shown that receptors for  $\Gamma$ -aminobutyric acid (GABA) or GABA-mimetics are responsible for the settlement of the red abalone *Haliotis rufescens* (Morse and Morse 1984, Baxter and Morse 1987, Trapido-Rosenthal and Morse 1986). There is evidence that ammonia produced by beds of oysters induces settlement (Khalil et al. 1988, Coon et al. 1988). The data in this study, particularly concerning Greenwich Cove/Greenwich Bay, show that large numbers of juveniles are not coincident with large numbers of adults, nor are large numbers of adults coincident with large numbers of juveniles. Thus for *Mercenaria*, chemical cues (or pheromones) from the adults may not be a major factor in the initiation of settlement. The possibility of chemical cues inhibiting settlement in *Mercenaria* is not excluded.

The presence of large numbers of adult quahogs in Greenwich Cove may be a factor in the recruitment of juvenile quahogs in Greenwich Bay. The average density of *Mercenaria* in the portion of Greenwich Cove sampled for this study was about 190/m<sup>2</sup>. Greenwich Cove is 106.8 ha, assuming that the average density of quahogs in all of Greenwich Cove is 25% of the sample area, there would be a standing crop in excess of 50 million individuals. The shell-free wet weight biomass of this many quahogs would be approximately 0.5 million metric tons (Fig. 5).

Quahogs harvested from very dense beds well inside Greenwich Cove have been harvested as part of a state sponsored transplant program (Ganz 1987). As stated earlier, little has been done previously to evaluate the reburrowing of quahogs harvested and translocated under these relay programs. Our data suggest that all quahogs less than 83 mm in valve length were able to reburrow within a

week. Quahogs exceeding 83 mm show the lowest capability of reburrowing. These quahogs have the lowest direct commercial value but are potentially quite fecund. It might be argued on this basis that transplants from some dense, predominantly adult assemblages may reduce the production of larvae destined for settlement in actively exploited shellfish grounds. Further research is necessary to evaluate the maintenance of "spawner sanctuaries" and transplant programs as tools for shellfish management.

As previously noted, there have been several studies which have shown that population numbers and growth of *Mercenaria* is greater in sediments which have a lower percentage of silts and clay muds. We speculate that the process of fishing in Greenwich Bay resuspends sediments and results in a higher percentage of sands. This may be an explanation for the slightly lower silt/clay fraction in Greenwich Bay sediments (Table 1). This slightly higher sand content of the Greenwich Bay sediments may be another factor in the increased settlement and survival of juvenile *Mercenaria*. As early as the 1900s, bottom cultivation or stirring the sediments to allow fine silts and clays to drift away with the currents has been promoted and practiced as a means of enhancing the settlement of various species of bivalves (Belding, 1931; Rask, 1986). Controlled experiments are necessary to confirm the anecdotal observations of the efficacy of bottom cultivation.

In summary, we have shown that intensive commercial and recreational shellfishing results in significant changes in the population structure of *Mercenaria*. The shellfishing results in lowered numbers of mature adults and enhances the settlement and/or survival of juveniles. The exact mechanism for enhancement of settlement and/or survival of juvenile *Mercenaria* is not understood. Further studies are necessary to elucidate the relative effects of adult removal and sediment disturbance.

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#### REFERENCES

- Baxter, G. & D. E. Morse. 1987. G protein and diacylglycerol regulate metamorphosis of planktonic molluscan larvae. *Proc. Natl. Acad. Sci. USA* 84:1867-1870.
- Belding, D. 1931. The quahog fishery of Massachusetts. Massachusetts Department of Conservation, Marine Fisheries Series Leaflet No. 2.
- Black, R. & C. H. Peterson. 1988. Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal macroinvertebrates. *J. Exp. Mar. Biol. Ecol.* 120:183-198.
- Broom, M. J. 1982. Analysis of the growth of *Anadara granosa* (Bivalvia: Arcidae) in natural, artificially seeded and experimental populations. *Mar. Ecol. Prog. Ser.* 9:69-79.
- Butman, C. A. 1986. Larval settlement of soft-sediment invertebrates: Some predictions based on an analysis of near-bottom profiles. *In:*

- J. C. J. Nihoul (ed.). Marine Interface Ecohydrodynamics, Elsevier Science Publishing Co., New York, 670 pp.
- Campbell, R. 1961. A summary report of the fleet plotting program in Narragansett Bay. Rhode Island Division of Fish and Game Leaflet No. 4.
- Castagna, M. 1984. Methods of growing *Mercenaria mercenaria* from post-larval to preferred-size speed for field planting. *Aquaculture* 39:355-359.
- Coon, S. L., M. Walsh, W. K. Fitt, D. B. Bonar & R. M. Weiner. 1988. Induction of settlement behavior in oyster larvae by ammonia. *Am. Zool.* 28:70A (abstract).
- Dettmann, E. H., J. F. Paul, J. S. Rosen & C. J. Strobel. 1989. Transport, fate and toxic effects of a sewage treatment plant effluent in a Rhode Island estuary. Report no. 1003 Environmental Research Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Narragansett, RI. 134 pp.
- Ertman, S. C. & P. A. Jumars. 1988. Effects of bivalve siphonal currents on the settlement of inert particles and larvae. *J. Mar. Res.* 46:797-813.
- Folk, R. L. 1968. Petrology of Sedimentary Rocks. University of Texas, Austin. 170 pp.
- Ganz, A. R. 1987. Shellfish stock relocations: The Greenwich Bay experience. Narragansett Bay Symposium, April 22-25, 1987. p. 113.
- Grizzle, R. E. & R. A. Lutz. 1988. Descriptions of macroscopic banding patterns in sectioned polished shells of *Mercenaria mercenaria* from southern New Jersey. *J. Shellfish Res.* 7:367-370.
- Grizzle, R. E. & R. A. Lutz. 1989. A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. *Mar. Biol.* 101:95-105.
- Gross, M. G. 1972. Marine waste deposits near New York. *Mar. Poll. Bull.* 3:61-63.
- Hancock, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer 164:113-131.
- Hunt, J. H., W. G. Ambrose, Jr. & C. H. Peterson. 1987. Effects of the gastropod, *Ilyanassa absoleta* (say), and the bivalve, *Mercenaria mercenaria* (L.), on the larval settlement and juvenile recruitment of infauna. *J. Exp. Mar. Biol. Ecol.* 108:229-240.
- Khalil, A., W. K. Fitt, S. L. Coon & D. B. Bonar. 1988. Production of ammonia by fed and starved oysters *Crassostrea gigas* in relation to metabolism and metamorphosis. *Am. Zool.* 28:122A (abstract).
- Knight, W. 1968. Asymptotic growth: An example of nonsense disguised as mathematics. *J. Fish. Res. Board Can.* 25:1303-1307.
- Kovach, K. A. M. 1968. Shellfish Survey of Wickford Harbor. Rhode Island Division of Fish and Game Leaflet No. 24.
- Kovach, K. A. M., M. T. Canario & G. Gray. 1968. Shellfish Survey of the West Passage of Narragansett Bay. Rhode Island Division of Fish and Wildlife Leaflet No. 26.
- Meadows, P. S. & J. I. Campbell. 1972. Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.* 10:271-382.
- Morse, A. N. C. & D. E. Morse. 1984. Recruitment and metamorphosis of *Haliotis* larvae are induced by molecules uniquely available at the surfaces of crustose red algae. *J. Exp. Mar. Biol. Ecol.* 75:191-215.
- Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monogr.* 52:437-475.
- Peterson, C. H., P. B. Duncan, H. C. Summerson & B. F. Beal 1985. Annual band deposition within shells of the hard clam, *Mercenaria mercenaria*: Consistency across habitat near Cape Lookout, North Carolina. *Fish. Bull.* 83:671-677.
- Peterson, C. H. & R. Black. 1987. Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. *Limnol. Oceanogr.* 32:143-166.
- 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. & D. A. Campbell. 1956. Environmental factors affecting growth in *Venus mercenaria*. *Limnol. Oceanogr.* 1:2-17.
- Pratt, S. D. 1988. Status of the hard clam fishery in Narragansett Bay. Draft Report—Narragansett Bay Project, U.S. Environmental Protection Agency. 89 pp. + 26 figures.
- Rask, C. 1986. The effect of hydraulic harvesting on sediment characteristics related to shellfish abundance. Massachusetts Cooperative Extension Leaflet, Barnstable, Massachusetts.
- Ricketts, E. F., J. Calvin & J. W. Hedgpeth. 1968. Between Pacific Tides. (4th ed.). Stanford University Press, Stanford, California, 614 pp.
- Saila, S. B., J. M. Flowers & M. T. Canario. 1967. Factors affecting the relative abundance of *Mercenaria mercenaria* in the Providence River, Rhode Island. *Proc. Natl. Shellfish. Assoc.* 57:83-89.
- Saila, S. B., C. W. Recksiek & M. H. Prager. 1988. Fishery Science Application System (FSAS). BASIC Fishery Science Programs: A Compendium of Microcomputer Programs and Manual of Operation. Elsevier Scientific Press, Amsterdam. 230 pp.
- Sisson, R. T. 1976. Hard clam resource assessment study in the upper Narragansett Bay and the Providence River, Rhode Island. Rhode Island Division of Fish and Wildlife Leaflet No. 49.
- Spaulding, M. & C. Swanson. 1984. Tides and Tidal Currents of Narragansett Bay. Sea Grant Marine Technical Report No. 35, The University of Rhode Island, Narragansett Bay Campus.
- Stickney, A. P. & L. D. Stringer. 1957. A study of the invertebrate bottom fauna of Greenwich Bay, Rhode Island. *Ecology* 38:111-122.
- Trapido-Rosenthal, H. G. & D. E. Morse. 1986. Availability of chemoreceptors in down-regulated by habituation of larvae to a morphogenetic signal. *Proc. Natl. Acad. Sci. USA* 83:7658-7662.
- Walker, R. L. & K. R. Tenore. 1984. The distribution and production of the hard clam, *Mercenaria mercenaria* in Wassaw Sound, Georgia. *Estuaries* 7:19-27.
- Williams, J. G. 1980. The influence of the adults on the spat of the clam, *Tapes japonica*. *J. Mar. Res.* 39:735-743.
- Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *J. Mar. Res.* 24:25-41.