Aspects of the Biology of the Northern Quahog, *Mercenaria mercenaria*, with Emphasis on Growth and Survival during Early Life History

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**Abstract.** Key features of the biology of Mercenaria mercenaria are reviewed with emphasis on early life history processes. Predatory mortality during juvenile stages of the northern quahog is identified as a primary factor controlling recruitment of natural populations. Predation rates are shown to be strongly modulated both by substrate preference and prey-size selectivity of major predators (crabs and carnivorous gastropods). Smaller xanthid crabs prefer heterogeneous substrates (gravel and shell bottoms), and consume quahogs at a higher rate in these substrates, whereas larger, portunid crabs prefer and forage most effectively in homogeneous substrates. In contrast to predictions of optimal foraging theory, even larger crabs preferentially consume smaller quahogs, when a wide range of prey sizes is available, thus increasing predation pressure on smaller quahog size classes.

Under field conditions, at near-optimum temperatures, juvenile M. mercenaria exhibit mean shell growth rates of 0.8 mm week⁻¹ (maximum = 1 mm wk⁻¹). Native populations along the east coast exhibit comparatively lower and higher than average lifetime growth rates at the species’ northern (Prince Edward Island, Canada) and southern (Florida) distributional limits, respectively. These extremes correlate with the length of the growing season, which is strongly temperature-dependent. Thus, the time to attain legal market-size ranges from 1.9 to ≥ 6 years and averages three to four years in the mid-portion of the northern quahog’s latitudinal ranges (Massachusetts to Virginia). Up to a two- to three-fold variation in growth rates is typically observed within a single estuary. Three toxic/noxious algal species are identified as potentially harmful to M. mercenaria under bloom conditions: the chrysophyte Aureococcus anophagefferens, the chlorophyte Nannochloris atomus, and the dinoflagellate Alexandrium fundyense. Management implications and suggested fruitful directions for future research are discussed throughout the text.

**Introduction**

The biology of northern quahogs, *Mercenaria mercenaria*, has been the subject of several earlier (e.g. Belding, 1931) and more recent literature reviews (Pratt et al., 1992; Rice and Pechenik, 1992). Therefore this paper does not attempt an exhaustive review, but rather, will highlight some salient features of this species’ life history which are of significance in managing wild stocks. Processes operating during early life history stages (Figure 1) are emphasized, because recruitment success into the fishery appears to be largely predetermined during the clams' first one to two years of life (Malinowski, 1985; Wallace, 1991). Poorly understood aspects of the species' biology will also be stressed, in order to suggest avenues for future research.
Reproduction

*Mercenaria mercenaria* is a relatively slow-growing, long-lived, dioecious bivalve, characterized by iteroparity (multiple reproductions over its lifespan), high fecundities, production of planktotrophic larvae that typically remain in the plankton for one to two weeks (Carriker, 1961), and high juvenile relative to adult survival (Malinowski and Whitlach, 1988). Important life history characteristics of this species are summarized in Table 1. Aging techniques rely on the presence of annual growth checks in the shell, which are typically produced during the winter in the northern and central portion of the northern quahog's geographic range, and in the summer and early fall in southeastern states (North Carolina, Georgia, and Florida) (Fritz and Haven, 1983; Grizzle and Lutz, 1988; and references therein). Longevity estimates for the species range widely between 23 and 46 years because of the difficulty in aging older specimens, which show crowding of growth rings and numerous spurious growth checks. Maximum size ranges between 110-111 mm in shell length (Rice et al., 1989; Jones et al., 1989) and 135 mm (Walker and Tenore, 1984). A long lifespan, and the coexistence of multiple year classes, will tend to buffer hard clam populations from sudden population crashes caused by sporadic recruitment failure.

Fecundity, as determined by repeated spawning induction of mature individuals in the laboratory, is positively correlated with body size, but highly variable among individuals of the same size (Table 1). *M. mercenaria* shows no evidence of reproductive senility, or decline in reproductive output or gamete viability with age/size (Bricelj and Malouf, 1980), since older clams produce gametes at a level predicted by the power curve relating gonad mass to body size in younger individuals (isometric growth) (Peterson, 1986). Bricelj and Malouf (1980) showed that mature eggs spawned at one time by a single female are characterized by a bimodal size-frequency distribution, with modal peaks at 67 and 81 μm in diameter (range = ca. 50 to 97 μm). This was confirmed by Gallager and Mann (1986), who found that quahog eggs separated into three distinct bands following density gradient centrifugation. The significance of this wide range in egg sizes has not been determined. Since egg size in *M. mercenaria* is known to be positively correlated with egg lipid content (Gallager and Mann, 1986), eggs of different sizes may be characterized by different development times (Clarke, 1982) or differential viability. Thus Kraeuter et al. (1982) found that smaller eggs (< 35 μm) had significantly lower survival than eggs > 44 μm.

Spawning of quahog populations is less synchronous and starts earlier in the year with decreasing latitude (Table 3.3 in Eversole, 1989). The length of the spawning season and the frequency of peak spawning periods also tend to increase with decreasing latitude. A single, annual spawning peak, occurring in the summer, is characteristic of northern and mid-Atlantic waters (e.g. Connecticut, New York, and Delaware), whereas two spawning peaks (in the spring and fall) occur in North and South Carolina (reviewed by Eversole, 1989), and a third winter spawning may occur in Georgia (Heffernan et al., 1989) and in Florida (Hesselman et al., 1989). Quahogs may retain a relatively high condition index after spawning (Ansell et al., 1964; Keck et al., 1975), and consequently do not experience the large fluctuations in meat quality and marketability...
<table>
<thead>
<tr>
<th>Table 1</th>
</tr>
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<tbody>
<tr>
<td>Life history attributes of <em>Mercenaria mercenaria</em></td>
</tr>
<tr>
<td>---------------------------------------------</td>
</tr>
<tr>
<td><strong>Source:</strong></td>
</tr>
<tr>
<td>Longevity (years) 40</td>
</tr>
<tr>
<td>46</td>
</tr>
<tr>
<td>36</td>
</tr>
<tr>
<td>23</td>
</tr>
<tr>
<td>Age at first sexual maturity (yrs.) 1</td>
</tr>
<tr>
<td>Length at first sexual maturity (mm) 22-26</td>
</tr>
<tr>
<td>33</td>
</tr>
<tr>
<td>37</td>
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<tr>
<td>Mean diameter of spawned eggs (μm) 67-81</td>
</tr>
<tr>
<td>81-82</td>
</tr>
<tr>
<td>Fecundity (x 10^6 eggs clam^-1):</td>
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<tr>
<td>Mean</td>
</tr>
<tr>
<td>Sublegal 1.6</td>
</tr>
<tr>
<td>^a Littlenecks 2.8</td>
</tr>
<tr>
<td>^b Cherrystones 7.1</td>
</tr>
<tr>
<td>^c Chowders 6.3</td>
</tr>
<tr>
<td>Cherrystones &amp; Chowders 8.6</td>
</tr>
<tr>
<td>Calculated from Ansell, 1967</td>
</tr>
<tr>
<td>Calc. from Davis &amp; Chanley, 1956</td>
</tr>
<tr>
<td>Littlenecks 1.9</td>
</tr>
<tr>
<td>Knaub &amp; Eversole, 1988</td>
</tr>
</tbody>
</table>

Commercial size classes from Greene (1978):  
^a 48.0 ≤ L ≤ 70.5; 25.4 ≤ T ≤ 36.1  
^b 70.5 ≤ L ≤ 80.2; 36.1 ≤ T ≤ 40.8  
^c L > 80.2; T > 40.8, where L = shell length and T = thickness, in mm.

associated with changes in the reproductive cycle which are typically observed in oysters, *Crassostrea* spp. (e.g. Purdue et al., 1981).

Settlement of quahog larvac is highly gregarious, and is stimulated by the presence of conspecifics (e.g. 3 mm juveniles) or other clam species such as *Gemma gemma*, which often occurs at high densities in *Mercenaria* habitat (Ahn, 1990). This attraction appears to be chemically mediated (Keck et al., 1974; Ahn, 1990). In the field, larval settlement and/or retention of postlarvae may be enhanced in shell-covered sediment, which could provide a suitable attachment substrate and/or refuge from predators (Carriker, 1961), but this effect has not been rigorously tested under field or laboratory conditions. Flume studies show that selection capabilities of quahog larvac for a suitable
settlement substrate (i.e. preference for sand vs. mud) are affected by flow conditions (Butman et al., 1988), but the relevance of this finding to field conditions has not been demonstrated. Studies of settlement success and post-settlement survival of quahogs have been hindered primarily by the difficulty in efficiently segregating postlarvae from sediment grains of comparable size. Differential settlement was successfully used by Ahn (1990) in small-scale experiments, but may not be practical for large-scale sampling of a patchy natural environment.

Interactions between adult, benthic populations, through suspension-feeding activity or reworking and destabilization of sediments, and quahog larvae are poorly understood. Kurkowski (1981) demonstrated that adult quahogs can readily consume young veliger larvae < 120 μm in laboratory experiments, and that larvae do not survive entrapment in pseudofeces. A negative interaction between adult Mercenaria stocks and settlement was also suggested by Rice et al. (1989), who documented much higher densities of juvenile quahogs in areas of Narragansett Bay, Rhode Island, with low adult densities.

Successful metamorphosis and post-settlement recruitment of hatchery-produced quahog larvae is known to be influenced by egg and larval quality, as measured by their lipid content (Gallager et al., 1986; Gallager and Mann, 1986). These authors found that survival of quahog and oyster larvae to the pediveliger stage was invariably poor when egg lipid levels were low (< 18% of the ash-free dry weight), but that high egg lipid content could result in both high and low survival. A similar relationship was described between larval lipid content and survival through metamorphosis (Gallager et al., 1986). These results indicate that lipid content alone is not always a reliable predictor of gamete quality and larval survival. It also remains to be determined whether naturally occurring egg and larval populations commonly experience lipid levels below the minimum threshold which was established as prerequisite for larval survival in the laboratory.

Natural Mortality: Predation

Predation is often considered the most significant source of natural mortality, and thereby the dominant factor controlling recruitment success of naturally occurring bivalves, including Mercenaria mercenaria (e.g. Virmstein, 1977; Malinowski, 1985). Vulnerability to predation is known to be strongly size-dependent, with smallest quahogs (< ca. 20 mm in shell length) suffering greatest mortalities (MacKenzie, 1977; Malinowski, 1985). Furthermore, modeling efforts by Malinowski and Whitlach (1988) demonstrated that population growth rates of quahogs were two to four orders of magnitude more sensitive to changes in juvenile survivorship, than to those in adult survival or fecundity. These authors therefore suggested that stock enhancement measures would be most effective when directed towards enhancing juvenile survival (e.g. through predator control). In this context, Peterson (1990) recently argued convincingly for the need to apply experimental data on size selectivity and habitat preference of bivalve predators to fishery management and resource enhancement efforts.

Effect of Prey Size

Newly settled clams are expected to be highly vulnerable to predation because they are asiphonate and must feed at the sediment-water interface. Information on predation of early post-settlement stages is extremely limited, however, and largely qualitative (reviewed by Gibbons and Błogosławski, 1989). Losses during later, juvenile stages are better documented, but have rarely been determined by sampling of natural populations because quahogs < 20 mm in length are inefficiently captured by most commonly used sampling gear, e.g. quahog shell buckets. MacKenzie (1977), however, was able to provide strong evidence of high predatory mortalities at smaller sizes in Great South Bay, New York and Horseshoe Cove, New Jersey, by determining the relative proportion of dead and live quahogs collected with a diver-operated hydraulic suction dredge. He also used
distinctive shell markings to attribute deaths to specific predator groups (various gastropods, crabs, and starfish). This approach, when used in commercially exploited areas, is obviously only reliable to determine natural mortality rates of quahogs below legal harvestable size. It also tends to underestimate the number of dead quahogs, because crabs often break shells, especially of smaller prey, to irretrievable fragments. Evidence of greater predation pressure on smaller sizes is therefore mostly generated from field plantings of quahogs of varying sizes (e.g. Malinowski, 1985; Flagg and Malouf, 1983; Peterson, 1990).

Crabs, carnivorous gastropods, and starfish are the three most important groups of predators of quahogs, although finfish (e.g. rays) are known to be significant predators south of Delaware Bay (Krautter and Castagna, 1980). *M. mercenaria* attains complete size refuge from oyster drills, and most crabs, including spider crabs, rock crabs, green crabs, and mud crabs (*Dyspanopeus sayi*) at a shell length $\geq$ 30 mm (Figure 1). Quahogs $< 40$ mm remain vulnerable to two of the larger crabs species, the mud crab *Panoepus herbstdii* and blue crab, *Callinectes sapidus*, which attain maximum sizes of ca. 62 mm and 227 mm in carapace width (CW) respectively (Williams, 1984). Susceptibility to predation is inversely related to quahog size because both the number of potential predators (Figure 2), and the number of prey consumed by any given predator size class (e.g. Peterson, 1990) decline with increasing prey size.

Burrowing, predatory gastropods such as whelks and moon snails are the most important predators of adult quahogs $> 40$ mm in shell length (Figure 1). Gastropods (including oyster drills) are highly specialized predators that feed almost exclusively on bivalves, and leave distinct markings on their shells. However, they are relatively slow moving and thus cannot rapidly invade an area following natural (e.g. salinity disturbance) or man-induced eradication. Wide dispersal is further limited by the lack of a free-swimming early developmental stage, except in the case of moon snails. Gastropods also exhibit long prey handling times, and consumption rates for quahogs that are typically two to three orders of magnitude lower than those of crabs [e.g. $\leq 1$ quahog week$^{-1}$ for whelks and moon snails (Carriker, 1951; Greene, 1978)]. Whelks preferentially feed on larger quahogs ($> 40$ mm), and both whelks and moon snails show preference for thin-shelled bivalves, when alternate prey is available (Carriker, 1951). Nevertheless, whelks are known to be major predators of adult *Mercenaria* in North Carolina (Peterson, 1982; Irlandi and Peterson, 1991), and can account for up to 13 percent annual losses of the quahog population in Great South Bay, New York (Greene, 1978). Starfish can only prey on large quahogs in aggregation (Doering, 1981), and are more effective predators of epifaunal than infaunal bivalves (e.g. oysters, mussels, and scallops).

Due to their motility, high predation rates, and high relative abundance, crabs are deemed the most serious predators of smaller quahogs. They are generally able to consume quahogs of shell lengths up to 30 percent of their CW, although *Panoepus herbstdii*, which feeds on quahogs up to 65 percent of its CW, provides an exception to this rule of thumb (MacKenzie, 1977; Whetstone and Eversole, 1981; Gibbons and Blegoslawski, 1989). The high vulnerability to predation of quahogs $< 20$-25 mm in length is aggravated by the fact that even larger crabs, that are not mechanically constrained to feed on small prey, select smaller quahogs when a wide size range is available. For example, large blue crabs ($> 125$ mm in CW) preferentially prey on 10-25 mm *M. mercenaria*, when offered quahogs ranging in size from 5 to 35 mm, both in the presence and absence of sediment (Peterson, 1990). Their consumption rates (number of prey eaten per unit time) for 30-35 mm quahogs are 5 times lower than those for 10-15 mm quahogs. A similar preference for smaller quahogs was shown for the large mud crab, *Panoepus herbstdii* (Whetstone and Eversole, 1981), although energy intake (tissue weight of quahogs consumed per unit time), was maximized at larger sizes.

Selection for smaller prey appears to be a general phenomenon among crustaceans.
Figure 2. Maximum size (shell length in mm) of hard clams consumed by twelve common predators of Mercenaria mercenaria in east coast estuaries.

Sources:
P. longicarpus (hermit crab)  Gibbons, 1984
Libinia sp. (spider crab)  Gibbons & Blogoslawski, 1989
D. (Nooranops) sayi (mud crab)  Carriker, 1961; Gibbons, 1984
C. irroratus (rock crab)  MacKenzie, 1977
O. ocellatus (calico crab)  Gibbons & Blogoslawski, 1989
C. maenas (green crab)  MacPhail et al. 1955 & Taxisarchis, 1955
in Gibbons & Blogoslawski, 1989
P. herbstii (mud crab)  Wheistone & Eversole, 1981
C. sapidus (blue crab)  Arnold, 1984
Eupleura caudata & Urosalpinx cinerea (oyster drills)  MacKenzie, 1977
P. duplicatus (moon snail)  Carriker, 1951; Greene, 1978
Busycon canaliculatum (whelk)  Carriker, 1951; Greene, 1978
Asterias forbesi  Doering, 1981

(primarily crabs) feeding on hard-shelled mollusks, and occurs even when larger prey are more profitable in terms of energy yield per unit time (Juanes, 1992). This discrepancy between empirical data and classical optimal foraging theory, which predicts preference for prey that maximize the predators' net energy gain, may be related to greater claw damage and fitness costs associated with handling of larger prey (Juanes and Hartwick, 1990).
Effect of Substrate Type

Characterization of the predator assemblage at a given site, and an understanding of the effects of environmental factors (e.g. temperature and substrate type) on feeding rates of key predator species are important in explaining and predicting site-specific differences in population abundance of quahogs, and in implementing resource enhancement management strategies (e.g. habitat manipulation). The effects of sediment type on quahog predatory mortalities have only been studied in the laboratory or small-scale field trials; their outcome depends to a large extent on the species composition, abundance, size structure, and substrate preference of existing predators.

Seagrasses were shown to enhance survival of infaunal prey that can burrow beneath the root-rhizome mat, such as quahogs, by reducing the foraging effectiveness of whelks (Peterson, 1982). Whelks are also generally absent from shell-covered bottoms, which inhibit their burrowing activity (WAPORA, 1981). Crabs typically show highest predation rates in their preferred substrates. This generalization will be illustrated below for two major groups of quahog predators, the large swimming crabs (Portunidae), such as blue crabs (Callinectes sapidus) and calico crabs (Ovalipes ocellatus), and for the smaller mud crabs (Xanthidae). The former prefer homogeneous substrates (sand or mud/sand combinations) to crushed shell or gravel (20 to 50 mm in diameter) (Figure 3A). Given an equal density of quahogs among substrates, they also prey most heavily on their preferred substrate (Figure 3B).

Reduced foraging efficiency of *O. ocellatus* in gravel was related to increased searching time and handling of non-prey items in this substrate (Sponaugle and Lawton, 1990). This behavioral response provides the basis for the recommended use of gravel or crushed stone aggregate in quahog growout sites in southeastern states such as Virginia, where blue crabs are prevalent (Castagna and Kretz, 1977). Abundance and therefore predation intensity by large, highly mobile portunid crabs (e.g. blue crabs) is expected to be temporally much more variable, especially in areas that are at the limit of their distributional range, than that of mud crabs, which form less mobile, gregarious populations that persist from year to year.

Mud crabs are often the numerically dominant crabs in east coast estuaries. *Dyspanopeus sayi* is most abundant north of Delaware Bay, attaining densities of up to 100 crabs m⁻² (WAPORA, 1981), whereas *Eurypanopeus depressus* and *Panopeus herbstii* are prevalent in Chesapeake Bay and the Carolinas respectively (Day, 1987). Field surveys reveal that the three species are found at highest densities in heterogeneous substrates (gravel, or bottoms with shell, eelgrass or *Spartina* cover) (WAPORA, 1981;

![Figure 3](image-url)

**Figure 3.** (A) Results of blue crab (*Callinectes sapidus*) substrate preference tests, in which the location of a crab with respect to sediment type was determined in a series of laboratory paired (2-choice) comparisons (drawn from Arnold, 1984).

(B) Predation rate (mean ± standard error) of blue crabs and calico crabs on Mercenaria mercenaria in various substrates, determined in the laboratory (drawn from Sponaugle & Lawton, 1990) (see sources for further details).
Day and Lawton, 1988). In agreement with field data, and in contrast to the larger portunid crabs, laboratory trials show that mud crabs (D. sayi, E. depressus, and P. herbstdii) prefer heterogeneous substrates, especially crushed shell, to sand or mud (Day, 1987). Predation rates of D. sayi on juvenile quahogs were found to be significantly greater in small (<17 mm diameter) or large (>30 mm) gravel than in sand (Day, 1987), thereby lending support to the observation that substrate preference and predation pressure are positively correlated, and illustrating that habitat structural complexity is not always associated with a reduction in foraging efficiency. Flagg and Malouf (1983) also found that survival of field-planted juvenile quahogs in areas where mud crabs were abundant, was inversely correlated with gravel size ranging between 6 and 32 mm in diameter.

This preference for substrates with a complex topography appears to be related to the mud crabs' small adult size (e.g. D. sayi attains only 28 mm in CW), and thus requirement for refuge from top predators (bottom-feeding fish). Consumption of juvenile quahogs by D. sayi, for example, is strongly inhibited by increased predatory risk in the presence of toadfish, Opsanus tau (Day, 1987). Introduction of this fish species has therefore been suggested as a method of biological control of predation in quahog growout sites (Gibbons and Castagna, 1985).

Effect of Prey Density

A strong, predator-mediated, negative correlation between population density and survivorship of M. mercenaria has been demonstrated during juvenile but not adult stages (Malinowski, 1985). Average seasonal survivorship in eastern Long Island was four times greater at a density of 100 juvenile quahogs m\(^{-2}\) than at 1200 quahogs m\(^{-2}\). In this study, quahog density had a greater effect in explaining juvenile survival at two sites where crustaceans were the dominant predators, than all other combined variables tested (quahog size, time of year, and location). Predation during juvenile stages was thus attributed a dominant role in maintaining the low densities characteristic of quahog populations.

Low density may thus provide infaunal prey populations with a mechanism for persistence even when subject to intense predation (Eggleston et al., 1992). Sponaugle and Lawton (1990) suggested that juvenile quahogs achieve a relative refuge from predation by calico crabs at low densities, in heterogeneous (sand/shell) substrate, but not in sand. In contrast, Peterson (1982) found no low density refuge, over the range seven to 28 quahogs m\(^{-2}\), for adult quahogs preyed upon by whelks. Thus refuge value at low densities may be predator- and habitat-specific.

Growth

The time required for seed clams to achieve size refuge from most predators will be effectively determined by their growth rate. Growth data for clams < one year old, sampled from natural populations, may be biased by size-selective predation or sampling efficiency, and are thus more readily derived from land-based culture systems or field enclosures that exclude predators. Growth rates of seed clams reared in the laboratory under optimal temperature and food conditions average about 0.58 mm week\(^{-1}\) can be realized with natural seston at near-optimum temperatures (17 to 28\(^{\circ}\)C) (Table 2). However, lower values (e.g. 0.45 to 0.62 mm week\(^{-1}\) are typically obtained when averaged over the entire growing season (e.g. Eldridge et al., 1979).

Table 3 lists some of the factors which have been shown to significantly influence growth of quahogs (see Rice and Pechenik, 1992 for a more extensive review). Temperature and sediment type are two of the environmental variables most frequently correlated with growth of M. mercenaria. Growth is generally greater in coarse-grained (sand or silty sand) than in fine-grained sediments. However, the effects of substrate type per se cannot be readily decoupled from the effects of flow velocity, and the quality and quantity of the overlying seston. Growth rate is consistently reduced at high suspended
Table 2

Growth rates of juvenile *Mercenaria mercenaria* exposed to natural seston (*L₀* and *L₉* = initial and final shell length in mm). Maximum (subtidal and density-independent) growth rates were selected where several conditions were tested. Growth rates were determined in enclosures in the natural environment unless otherwise noted.

<table>
<thead>
<tr>
<th>Site/Period</th>
<th>Shell Length (<em>L₀</em> - <em>L₉</em>)</th>
<th>Temp. (°C)</th>
<th>Growth Rate (mm/wk)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Napeague Harbor, NY; July-Aug.</td>
<td>10.3 - 14.2</td>
<td>22 - 28</td>
<td>0.96</td>
<td>Bricelj &amp; Borrero, unpubl.</td>
</tr>
<tr>
<td>Great South Bay, NY; Oct.-Nov. (raceways)</td>
<td>10.5 - 15.4</td>
<td>27</td>
<td>0.54</td>
<td>Bricelj, unpubl.</td>
</tr>
<tr>
<td>Fishers Island, NY; Aug. (land-based upwellers)</td>
<td>4.6 - 5.7</td>
<td>22</td>
<td>1.05</td>
<td>Appelmans, 1989</td>
</tr>
<tr>
<td>Shinnecock Bay*, NY; July-Oct.</td>
<td>7.9 - 15.4</td>
<td>-</td>
<td>0.62</td>
<td>Flagg &amp; Malouf, 1983</td>
</tr>
<tr>
<td>Folly River, SC; Feb.-Aug., May (raceways)</td>
<td>3.9 - 16.9</td>
<td>8 - 32</td>
<td>0.48</td>
<td>Hadley &amp; Manzi, 1984</td>
</tr>
<tr>
<td>Clark Sound,* SC; May-Dec.</td>
<td>13.0 - 26.9</td>
<td>-</td>
<td>0.45</td>
<td>Eldridge et al., 1979</td>
</tr>
<tr>
<td>Wassaw Sound*, GA (intertidal)</td>
<td>6.1 - 28.3</td>
<td>-</td>
<td>1.08</td>
<td>Walker, 1984</td>
</tr>
<tr>
<td>Alligator Harbor, FL; April</td>
<td>5.4 - 9.0</td>
<td>17 - 26</td>
<td>0.84</td>
<td>Menzel, 1963</td>
</tr>
</tbody>
</table>

Mean = 0.83

*Max. seasonal growth rate.

*Clams grown in substrate.

sediment loads (≥ 23 to 44 mg dry weight l⁻¹), whether these result from bioturbation (Murphy, 1985), or physical disturbance (wave action) (Turner and Miller, 1991).

Studies of the effects of seagrass habitat relative to unvegetated substrate on growth of *Mercenaria mercenaria* (reviewed in Table 3) have yielded conflicting results which may be related to site-specific differences in the flow regime, food concentrations, and structure of submerged aquatic vegetation. Positive effects have been attributed to increased near-bottom food supply to the benthos through enhanced particle settlement (Peterson et al., 1984), and resuspension or *in situ* production of benthic or epiphytic algae within the seagrass bed (Judge et al., in press), reduced siphon nipping activity by finfish (Coen and Heck, 1991), enhanced
Table 3.
Factors influencing growth of *Mercenaria mercenaria* (TOM = total organic matter; \( L_o \) and \( L_f \) = initial and final shell length). Positive or negative effects on growth are indicated, as well as the magnitude of growth inhibition, where appropriate.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Effect</th>
<th>Magnitude</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sediment type</td>
<td>Sand &gt; Mud</td>
<td>24%</td>
<td>(1)</td>
</tr>
<tr>
<td>(% silt-clay or TOM)</td>
<td>Sand &gt; Mud</td>
<td>( \leq 36% )</td>
<td>(2)</td>
</tr>
<tr>
<td></td>
<td>Sand &gt; Mud</td>
<td>( \leq 8% )</td>
<td>(3)</td>
</tr>
<tr>
<td>Suspended Sediments</td>
<td>(-)</td>
<td>16% at 44 mgDW l(^{-1})</td>
<td>(4)</td>
</tr>
<tr>
<td>Seston Flux</td>
<td>Max. growth at intermediate levels</td>
<td>(3,7)</td>
<td></td>
</tr>
<tr>
<td>Phytoplankton Concentration</td>
<td>(+) Diatoms&lt;15 ( \mu ) m</td>
<td>-</td>
<td>(2)</td>
</tr>
<tr>
<td>(+) Chlorophyll ( a )</td>
<td>-</td>
<td>(8)</td>
<td></td>
</tr>
<tr>
<td>Presence of Seagrass</td>
<td>(-)</td>
<td>-</td>
<td>(9,12)</td>
</tr>
<tr>
<td>(+)</td>
<td>-</td>
<td>(10,11,12)</td>
<td></td>
</tr>
<tr>
<td>no effect</td>
<td></td>
<td></td>
<td>(12)</td>
</tr>
<tr>
<td>Biological disturbance: siphon nipping</td>
<td>(-)</td>
<td>( \leq 25% )</td>
<td>(13)</td>
</tr>
<tr>
<td>Temperature</td>
<td>Range for (+) growth = 9-31°C</td>
<td>(2,14,15)</td>
<td></td>
</tr>
<tr>
<td>Optimum = 20-25°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Population Density</td>
<td>(-)</td>
<td>18% (80 clams m(^{-2}); (12) ( L_o = 5.8 \text{ cm} ))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-)</td>
<td>22% (190 clams m(^{-2}); (16) ( L_f = 6.2 \text{ cm} ))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-)</td>
<td>( \leq 19% ) (1159 clams m(^{-2}); (17) ( L_o = 1.3 \text{ cm}, L_f = 4.6-5.7 \text{ cm} ))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-)</td>
<td>33% (3027 clams m(^{-2}) (18) ( L_o = 1.7, L_f = 3.3 \text{ cm} ))</td>
<td></td>
</tr>
</tbody>
</table>


* Population density parameters include average length data.
sediment stability and reduced sediment resuspension (postulated by Irlandi and Peterson, 1991). Adverse effects may result from a reduction in horizontal seston flux (the product of seston concentration and current velocity) due to baffling of currents within the seagrass canopy (Irlandi and Peterson, 1991 and references in Table 3).

Differences in growth rate of *M. mercenaria* along the east coast of North America were described by Ansell (1968), who found no clear latitudinal pattern or correlation of growth rates with temperature in comparing populations between Massachusetts and Florida. Reduced growth occurs, however, near the species' northern distributional limit (Prince Edward Island, Canada), where lower temperatures result in a shorter growing season, and quahogs require six years or more to attain legal market size. The highest growth rates (time to market size = 2.2 years) have been recently reported for populations in Florida, where they are attributed to continued growth during the winter, and thus lengthening of the annual growing season at this latitude (Jones et al., 1990). These results were substantiated by Arnold et al. (1991) who noted that the mean growth parameter (the product of k and asymptotic size in the von Bertalanffy growth equation) was twice as high in the Indian River, Florida, than in Narragansett Bay, Rhode Island. Therefore *M. mercenaria* can achieve growth rates approaching those of faster growing clam species such as *Spisula solidissima* (surf clams) and *Mya arenaria* (softshell clams) (Fig. 2.5 in Malouf and Bricelj, 1989) only in the southern portion of its geographic range.

Table 4 compares growth rates of *M. mercenaria* populations, as reflected in the time required to attain legal market size. Ansell's (1968) data are extended or replaced where more current information is available. Minimum legal size is here assumed to be 25.4 mm in shell thickness, (the New York state limit), corresponding to a shell length of 48 mm based on morphometrics of quahog populations in Great South Bay (Greene, 1978), although the ratio of length to thickness may vary somewhat between locations. Populations between Maine and Georgia grow at comparable rates, typically requiring 3.0 to 4.4 years to attain market size (Table 4). Differences in growth rate among sites within an estuary are often greater than those among latitudes over a broader geographic scale (e.g. two-fold variation in Great South Bay (Greene, 1978), three-fold variation in Cape Lookout, North Carolina (Peterson and Beal, 1989), and 1.7- to two-fold variation in the $c_0$ parameter in the Indian River, Florida (Arnold et al., 1991) and Narragansett Bay, Rhode Island (Jones et al., 1989) respectively).

Population density of quahogs is generally not a significant factor influencing growth rates of natural populations (e.g. Malinowski, 1985). Density-dependent growth inhibition, generally only occurs during growout of cultured clams planted at densities two to three orders of magnitude greater than those found in nature (Table 3). Stunting of adult clams was found, however, in uncertificated waters in Greenwich Cove, Narragansett Bay, at unusually high natural densities of 190 clams m$^{-2}$ (Rice et al., 1989). Similarly, reduction in the condition index of adult clams occurred at experimental densities of 203 clams m$^{-2}$ (Malinowski, 1985).

Bulk measures of food quantity or phytoplankton biomass (chlorophyll $a$ concentration) may not necessarily provide a good predictor of bivalve growth, except under conditions of food limitation, which are not typically encountered in shallow, eutrophic estuaries. Thus, during virtually monospecific blooms of noxious (unpalatable, toxic, or indigestible) algae, bivalve populations may exhibit severe growth depression which may not be reflected in low or abnormal chlorophyll levels (e.g. Cosper et al., 1987). Correlations between food availability and growth can be improved by incorporating relevant measures of food quality (e.g. biomass of phytoplankton species known to support bivalve growth) (Pratt and Campbell, 1956).

Effect of Noxious Algal Blooms

Algal species which may adversely affect quahog populations under bloom conditions include: the chlorophyte *Nannochloris atomus,*
Table 4.

Average time (in years) to attain legal market size [= 48 mm in shell length (see text)] of *Mercenaria mercenaria* natural populations along the species' latitudinal range, from north to south. Range is shown between brackets; unless indicated, time to market size is calculated from fitted von Bertalanffy, Gompertz or logarithmic growth equations.

<table>
<thead>
<tr>
<th>Time (yrs.)</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.0</td>
<td>Prince Edward Island, Canada</td>
<td>Fig. 5 in Ansell, 1968</td>
</tr>
<tr>
<td>4.4</td>
<td>Maine</td>
<td>Fig. 5 in Ansell, 1968</td>
</tr>
<tr>
<td>3.2</td>
<td>Monomoy Point, Massachusetts</td>
<td>Fig. 5 in Ansell, 1968</td>
</tr>
<tr>
<td>4.0</td>
<td>Narragansett Bay, Rhode Island</td>
<td>1Jones et al., 1989</td>
</tr>
<tr>
<td>(3.0 - 4.8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.5</td>
<td>Great South Bay, New York</td>
<td>Appendix 4 in Buckner, 1984</td>
</tr>
<tr>
<td>(3.0 - 4.0)</td>
<td></td>
<td>Greene, 1978</td>
</tr>
<tr>
<td>(2.5 - 5.0)</td>
<td></td>
<td>1Kennish and Loveland, 1980</td>
</tr>
<tr>
<td>3.0</td>
<td>Barnegat Bay, New Jersey</td>
<td>From Table 5 in Kennish, 1980</td>
</tr>
<tr>
<td>4.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(3.8 - 4.6)</td>
<td>York River, Virginia</td>
<td>From Fig. 3 in Loesch and Haven, 1973</td>
</tr>
<tr>
<td>4.4</td>
<td>Core Sound, NC</td>
<td>2Peterson et al., 1983</td>
</tr>
<tr>
<td>2.4</td>
<td>Wassaw Sound, Georgia (intertidal)</td>
<td>Walker and Tenore, 1984</td>
</tr>
<tr>
<td>3.0 - 4.0</td>
<td>Kings Bay, southern GA</td>
<td>3Jones et al., 1990</td>
</tr>
<tr>
<td>2.0</td>
<td>Indian River, Atlantic coast of Florida</td>
<td>3Jones et al., 1990</td>
</tr>
<tr>
<td>2.2 - 2.3</td>
<td></td>
<td>Arnold et al., 1991</td>
</tr>
<tr>
<td>2.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1.9 - 2.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.6</td>
<td>Gulf Coast, Florida</td>
<td>Fig. 5 in Ansell, 1968</td>
</tr>
</tbody>
</table>

1. Shell height (H) converted to length using an H/L ratio = 0.933;
2. Assuming that age in years = number of annual bands;
3. Using a H/L conversion factor = 0.91.
the chrysophyte *Aureococcus anophagefferens*, and the dinoflagellate *Alexandrium fundyense*, the causative agents of "green," "brown," and "red" tides respectively. The first two species are picoplanktonic algae (circa 2 μm in diameter), which, due to their small size, are expected to be poorly retained by the clams' feeding apparatus. [Particle retention efficiency in *M. mercenaria* decreases steeply with decreasing particle size below a size of about four mm (Riisgård, 1988)].

Summer blooms of *N. atomus* were documented in Long Island's southern bays in the 1950's (reviewed by Ryther, 1989). Laboratory studies subsequently demonstrated that monospecific cultures of this alga do not support growth of quahogs in either larval (Tiu et al., 1989) or juvenile stages (Bass et al., 1990), and cause growth inhibition when combined with other algae of high nutritional value. Lack of growth on a monospecific diet of *N. atomus* was attributed to the quahogs' short gut retention and low absorption efficiency of ingested organics for this alga (Bricelj et al., 1984b).

*Aureococcus anophagefferens* first occurred in Narragansett Bay (Sieburth et al., 1988) and in eastern and southern Long Island bays in 1985 (Cosper et al., 1987), and has reappeared in New York waters in past years. This alga causes severe inhibition of quahog filtration rates (Tracey, 1988), and inhibition of ciliary beat in gill tissue excised from quahogs (Gainey and Shumway, 1991). The mechanism of this alga's toxigenic action is not yet clearly understood. Preliminary data suggest that although quahogs are less sensitive to the effects of *A. anophagefferens* than mussels, *Mytilus edulis*, they may still experience growth reduction at even moderate field concentrations of *A. anophagefferens* (1.1 x 10^8 to 3.2 x 10^8 cells liter^-1^) (Bricelj and Borrello, unpublished data).

Finally, *Alexandrium fundyense* and related species are responsible for the accumulation of paralytic shellfish poisoning (PSP) neurotoxins in suspension-feeding bivalves. *Mercenaria mercenaria* was found to accumulate low levels of PSP toxins during New England red tide outbreaks in 1972, when other similarly exposed bivalve species became highly toxic, presumably because blooms of highly toxic forms of this dinoflagellate elicit feeding depression and shell closure in this species (Twarog and Yamaguchi, 1974). Laboratory toxification experiments show, however, that *M. mercenaria* is capable of acquiring high levels of PSP toxins (2 to 3 orders of magnitude above the regulatory level for shellfish closures), when exposed to a Long Island, low-toxicity strain of *A. fundyense*, or a New England, high-toxicity dinoflagellate strain in combination with non-toxic phytoplankton (Bricelj et al., 1991). In conclusion, although the effects of blooms of these three algal species on naturally occurring quahog populations have not yet been determined, the experimental evidence indicates that they are at least capable of causing severe growth reduction, and could potentially cause mortalities of some life history stages under prolonged exposure.

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Questions and Answers

Q. (Mr. George DeBlois, shellfisherman) Have there been any studies to show how many spawners are needed to effectively repopulate an area, given predation, fishing, and other factors?

A. (Dr. Monica Bricelj, SUNY-Stony Brook) There has been some interest in trying to determine the minimum amount of stock necessary to sustain recruitment into the fishery. I know that there was a plan to do this kind of study in New Jersey, but I don't know if the plan was actually carried out. There is no published information at this time about minimum required broodstock, but there is some indirect evidence that might be considered. In the Great South Bay of Long Island, there has been a steady decline of the adult population. In spite of this, there has been no noticeable effect on the abundance of sublegal-sized clams (new recruits) between 1986 and 1989 in eastern Great South Bay, where survey data are available. Fishing has not appeared to lower the adult population below the critical minimum required to sustain recruitment. A decrease in the number of sublegal clams has been observed, however, in the last few years (1990 through 1992).

In terms of quahog growth, most studies have shown that the density of quahogs is not too important in limiting growth. In most areas, densities are somewhere between two to 15 animals per square meter. Generally it is rather rare to find natural populations of quahogs in densities of hundreds per square meter.

Greenwich Cove is one of the exceptional areas with very high adult densities. In these very high densities, lower growth or stunting has been shown. Density may have a major affect on recruitment, but this needs further study.
Q. (DeBlois) I have read that cherrystones produce many more eggs than the smaller littlenecks. Is there any evidence of a cessation of egg production as quahogs age?
A. (Bricelj) There is no evidence for this reproductive senescence in quahogs. Scallops are the only group of bivalves that I am aware of that have a reduction of gamete production with age. There is one important thing to be aware of. The studies which have shown that chowder quahogs are the most fecund are based upon laboratory examination of the number of gametes produced during induced spawning. We do not know how this reflects what is going on in the real world, in the sense that “How often do chowders spawn in nature?” But from the laboratory spawning experiments, there is no difference in the viability of eggs from littlenecks or chowders.

Q. (Prof. Dennis Nixon, URI) One of our objectives is increasing the stock, and my question is about predator control. About a hundred years ago there used to be a statute in Rhode Island that set a bounty on starfish, because of their recognized impact on shellfish populations. Do you believe that attempts at predator control in an open fishery such as in Narragansett Bay could be of any value?
A. (Bricelj) Well, Clyde MacKenzie of the National Marine Fisheries Service has suggested just this in the past, but people have balked at programs that would clear large areas such as the Great South Bay of predators. Economically it is not a very feasible solution. Perhaps in the context of smaller-scale areas, enhancement programs might work. Some type of habitat manipulation might be undertaken when we know which predator is most troublesome and what features of the substrate or other characteristics are important. Predator control is certainly important in nursery and growout phases of aquaculture. Predator control in open fisheries has not been tested except for MacKenzie’s work back in the mid-1970s. He did some predator eradication in relatively small plots and showed that there was a positive response, but there has been little further testing of this in the field. Eradication needs to be tested on a variety of scales to show just where it is effective. Eradication measures may be more effective at controlling moon snails or whelks, because they move slowly into an area. If you have highly motile predators such as blue crabs, it is doubtful that any eradication measures would work because they can come into an area so quickly. In brief, I think that any kind of eradication program must address predator type and scale.

Q. (Mr. John Finneran, shellfisherman) Is there any evidence showing that some sediments are more conducive to larval settlement than others? In other words, are there sediments that have a “better flavor” to settling larvae?
A. (Bricelj) Yes, there have been some laboratory studies on this. Keck and co-workers showed that if you treat sediment with “clam juice,” you will get an attractant response and increased larval settlement. This is a similar result to the data I presented which showed that juvenile clams exhibit an attractant response. It must be a chemosensory response, because sediments that were “pretreated” by placement of clams that were subsequently removed, also enhanced settlement. Physical factors may also play a role, since additions of gravel or clean clamshell to the sediment also increased settlement in this study.

Q. (Finneran) Are there any inorganics that might act as an attractant? I have noted that there are often large quahog assemblages in sediments that are high in coal ash.
A. (Bricelj) No, but one of the possible explanations for areas of high abundance in Great South Bay, might be the presence of shell fragments that modify the bottom topography making the area better for larval settlement and survival of juveniles. There has been no testing of this though. This is very difficult work. With oysters it is relatively easy, because they settle on hard surfaces like shells. Postset quahogs are in the size range of sediment particles, so nobody really wants to do this kind of tedious work. This kind of work is not intractable though, just difficult. One of the key things I want to
emphasize is that we need many more studies on
the early life history stages of quahogs rather
than adults. Year-class strength is being
determined by post-larval and juvenile survival.
These stages need more research attention.
Overview of Quahog Management Studies in Narragansett Bay, 1946 to 1992

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Abstract. There have been a considerable number of studies on quahog populations in Narragansett Bay that have provided valuable information for fisheries managers. Additionally, there have been a few socioeconomic studies that have characterized the labor force in the quahog fishery and have provided information pertinent to levels of fishing effort. Most ecological studies have focused on the population structure and standing crop densities of quahogs in Narragansett Bay. The age and growth rates of quahogs in different parts of Narragansett Bay are well known, but there is a dearth of information about the patterns of quahog recruitment. As with most fisheries that require little capital requirements, the levels of fishing effort in Narragansett Bay are known to increase or decrease with relative ease as conditions in the fishery or the general economy change. It is recommended that available socioeconomic data about the fishery be updated, and that studies be undertaken to assess the relative impacts of currently used fishing gear.

Introduction

It has been recognized by fisheries managers that a number of factors describing a fishery stock must be determined before one can begin to make any rational predictions about what levels of fishing effort are desirable for maintenance of a sustainable fishery (e.g. Royce, 1984). In simple terms, the inputs to a fishery stock are the recruitment of new individuals into the fishery and growth of individuals previously recruited into the fishery (Figure 1). Likewise, the factors which tend to reduce the size of fishery stocks are natural mortality of the stocks and the fishing mortality—a combination of the fishing catch plus associated mortality due to damage by gear etc. These basic principles of dynamic fishery stock models have been most frequently used for the management of finfish stocks, but with care can be applied to bivalve molluscan fisheries (Caddy, 1989).

Figure 1. The four key factors that determine quahog stock size.

One key aspect that distinguishes assessment of bivalve fisheries, such as the quahog fishery of Narragansett Bay, from assessment of finfisheries is that one is dealing with a sessile population of juveniles and adults. Additionally, quahogs and other bivalves are highly fecund, so that parental stock size is considered less important for recruitment than is available space, suitable
conditions for settlement, and postsettlement predation loss prior to recruitment into the fishery (Hancock, 1973; Kassner and Malouf, 1982; Malinowski and Whitlatch 1988; Malinowski, this volume). The end result of the various physical and biological factors determining quahog distribution is that fishery recruits are found in patches or clumps (e.g., Kassner et al., 1991). As a consequence of the patchiness in distribution of quahogs, special care must be taken to design appropriate sampling protocols that utilize appropriate statistical methods (e.g. Sall and Gaucher, 1966; Gardevers and Orrhage, 1968; Ludwig and Reynolds, 1988; Murawski and Serchuk, 1989). Techniques that may be appropriate for the sampling of quahogs in Narragansett Bay include transect or quadrat methodologies in coves and inlets (e.g. Rice et al. 1989) or stratified random sampling methods over wider areas (e.g. Russell, 1972; Murawski and Serchuk, 1989).

Recognizing that the sampling and statistical methods for quahogs may be different from those used for finfish stock assessments, it is the aim of this paper to outline key studies related to shellfish stock assessment that have been carried out in Narragansett Bay over the last 45 years, and to provide some insights into the areas where data is lacking. It should be noted that a recent report has been prepared that outlines in greater detail many of the studies covered in this paper (Pratt et al., 1992).

Figure 2. Locations of stations in Narragansett Bay from which quahogs were sampled for studies of growth rate. Triangles: Pratt and Campbell (1956); Squares: Jones et al. (1989); Circles: Rice et al. (1989).

and Campbell (1956) were able to collect very detailed information about the growth of quahogs from a number of locations around Narragansett Bay (Figure 2).

More recent studies have used the technique of sclerochronology (the assessment of age by quantification of periodic increments in the shell) for determining the age of quahogs (e.g. Rhoards and Panella, 1970; Kennish, 1980). Use of sclerochronology allows for the identification of individual year classes, which is otherwise difficult because quahogs are spawning throughout the summer and individual growth rates are highly variable.

By quantifying annual growth rings of quahogs from 10 stations in Narragansett Bay (Figure 3), Jones et al. (1989) were able to give a very detailed description of quahog growth as related to average annual water temperatures. One of their main findings is
minimum legal size (25.4 mm, 1 inch wide) by the end of its third growing season, and remains in the littleneck size category (25.4 to 38 mm wide) for four years after recruitment into the fishery. A recent comparison of growth data collected by Pratt and Campbell (1956) and the data of Jones et al. (1989) showed that although the methods were different and the studies were 33 years apart, the average growth rates of quahogs in Narragansett Bay were quite similar (Pratt et al., 1992). Additionally, a study done in North Carolina has validated the annual periodicity of bands in quahogs by use of a mark-and-recapture study (Peterson et al., 1983). Rice et al. (1989) also used sclerochronology to determine the growth rates of quahogs in dense adult assemblages in Greenwich Cove and West Passage (Figure 2). They found that quahogs in very dense assemblages grow at considerably lower rates than quahogs in less dense assemblages typified by the other growth studies. See Rice and Pechenik (1992) for a review of factors that may affect the growth of quahogs.

**Spawning and Recruitment**

The spawning of quahogs is known to be temperature dependent, and appears to be triggered as water temperatures approach 20°C (Loosanoff, 1937). Details of quahog fecundity and spawning are provided by Bricelj (this volume). A study based on plankton net tows in Narragansett Bay from 1950-1952 showed that the maximum numbers of quahog larvae in the water column were found during the summer months June to August (Landers, 1954). Since the larval period of quahogs can last approximately two weeks (Loosanoff et al., 1951), it is most probable that tidal currents and wind-generated surface waves can effectively disperse quahog larvae throughout Narragansett Bay (Wood and Hargis, 1971; Andrews, 1983). Thus, there need not be a necessity for a close proximity of broodstock to increase the level larval settlement and subsequent recruitment into the fishery.
Successful recruitment of quahogs is highly dependent on postsettlement survival of juveniles rather than absolute numbers of spawners producing gametes (Hancock, 1973; Malinowski and Whitlatch, 1988; Malinowski, this volume). Kassner and Malouf (1982) evaluated the practice of augmenting the numbers of broodstock in the Great South Bay, Long Island and found that there was no significant increase in quahog recruitment. Indeed, MacKenzie (1979) urged that the most effective means for increasing quahog recruitment is to protect juvenile quahogs from predation losses.

There have been few studies carried out in Narragansett Bay in which the rates of quahog recruitment have been determined. Juvenile quahogs have been quantified in some benthic surveys (e.g. Pratt, 1977), but these studies were not followed up to determine the rates at which postset juveniles reach legally fishable size. There have been two studies aimed at investigating the effects of fishing gear on the recruitment of quahogs. The first of these studies compared the relative impact of power dredging versus bullraking on the recruitment of quahogs (Glude and Landers, 1953). In the study area chosen for this study, there was little settlement or recruitment in control and test areas. Likewise, in a recent study by Sparsis and DeAlteris (details in this volume) designed to test the effects of bottom cultivation on the settlement and recruitment of quahogs, little settlement or recruitment of quahogs was noted in their test or control plots. The failure to find settlement and recruitment of quahogs in these studies during 1949-1950 and 1990-1991 suggests that there may be some paucity of quahog recruitment in some areas of Narragansett Bay. In another area of Narragansett Bay—Greenwich Bay, which is known to be one of the most productive areas for the quahog fishery—benthic studies suggest that there is annual recruitment of quahogs (Stickney and Stringer, 1957; Rice et al., 1989).

Assessments of Standing Stocks of Quahog

There have been a number of studies in the last 40 years aimed at mapping the location of quahog stocks and providing estimates of standing stock densities, but most have been confined to coves, inlets, and small portions of Narragansett Bay. A survey by Pratt (1953) carried out in 1949-1950 included 123 stations in Narragansett Bay, but the data were not mapped. The first Narragansett Bay-wide study that mapped the distribution of quahogs was based on a dredge survey between 1956 and 1957, undertaken in response to calls for the construction of mid-Bay hurricane barriers (Stringer, 1959). In this study, nearly 2,800 samples were taken on a 900-foot grid. Although the data from this study (Figure 4) were collected 35 years ago, the quahog distributions roughly approximate the general position of known stocks today. The last Narragansett Bay-wide study of quahog distributions was conducted jointly by the U.S. Environmental Protection Agency and the R.I. Division of Fish and Wildlife (1974). Maps of shellfish distribution were made, but there was no information provided as to stock abundance. The reason why large-scale surveys of quahog populations have been carried out only on an occasional basis is that these studies tend to be quite expensive.

Most quahog population studies have focused on coves or other subsections of Narragansett Bay. Quahog population studies were carried out by grab sampling in Greenwich Bay from 1951-1957 by the U.S. Fish and Wildlife Service and the R.I. Division of Fish and Game (Stickney and Stringer, 1957). At that time, maximum densities of quahogs were found in mixed sand and silt bottoms near the mouth of Greenwich Cove and near Mary's Creek (Figure 5). For a comparison, divers in 1988 using quadrat sampling methods found an average density of 190 quahogs/m² at the mouth of Greenwich Cove (Rice et al., 1989). Quantitative stock surveys have been carried
out in the closed areas of Providence River and the Upper Bay in 1956, 1965, 1976, and 1985 (Stringer, 1959; Campbell, n.d.; Canario and Kovach, 1965a; Sailer et al., 1967; Sisson, 1977; Pratt et al., 1987). In each of these studies, the population of quahogs in these areas was dominated by the presence of large adults, which typifies the population structure of quahogs in areas that have been closed to shellfishing for a long time (Figure 6).

In comparison to the numerous published studies which have focused on stocks in areas closed to shellfishing, there have been relatively few published studies on shellfish stocks in the areas of Narragansett Bay open to shellfishing. In addition to the previously cited Narragansett Bay-wide studies, Russell (1972) surveyed quahog populations in the West Passage of Narragansett Bay using dredge sampling techniques. A number of R.I. Department of Environmental
Management (R.I.D.E.M.)-sponsored studies are documented in the R.I. Division of Fish and Wildlife Leaflet Series. These R.I.D.E.M. surveys include the northern portion of Greenwich Bay (Campbell, 1959a); the Potowomut River (Campbell, 1959b); the Kickamuit River (Campbell 1959c; Canario, 1963); and the East Passage (Canario and Kovach, 1965b). In general, the population structure of quahogs in actively fished areas of Narragansett Bay differs from closed areas in that the fished areas have a predominance of younger, smaller quahogs. This distinction is best illustrated in a comparison study between actively fished and closed areas in Greenwich Bay and West Passage (Figure 7) (Rice et al., 1989).

Estimates of Natural Mortality

The first of the factors which remove individuals from quahog stocks is natural mortality. Natural mortality includes losses due to predation and diseases. It is known that pre-recruit juvenile quahogs are highly susceptible to predation losses. However, once quahog reach the size at which they recruit into the fishery, they are relatively resistant to most predators (e.g., Whetstone and Eversole, 1978; MacKenzie, 1979; Boulding and Hay, 1984).

Caddy (1989) outlines a method for estimating the natural mortality of bivalves by successively sampling the number of dead shells (paired valves) present in closed areas in relation to the number of live animals present. In the various studies of stock abundance in closed areas of Narragansett Bay, there has been no quantitative data collected as the levels of natural mortality in those areas. It is likely that natural mortality is relatively higher in
Estimates of Mortality Caused by Fishing

Estimates of the mortality of quahogs caused by fishing can be made by using estimates of standing crop abundances of quahogs and the number of quahogs caught. This method of estimating fishing mortality is highly dependent upon knowledge of the selectivity of the harvest gear. Using a "rocking chair" dredge, with catch efficiencies known for various substrate types, Russell (1972) estimated the fishing mortality of quahogs in the West Passage during one season of the commercial dredge fishery. During the dredge season, the standing crop of quahogs in his study area declined from 18,148 ± 5,704 bu to 7,235 ± 2,167 bu (1 bu = approximately 80 pounds or 31.5 kg). Breakage is important to consider as it may be a source of bias in fishing mortality estimates if catch alone is the sole basis of these estimates. One study in Narragansett Bay compared the effects of harvesting gear and handling on the breakage of quahogs (Glude and Landers, 1953). Broken quahogs caught in a "rocking chair" dredge ranged from 0.7% to 1.2% of the total catch. In rocky sediments, 2.9% of the remaining quahogs were found broken on the bottom, but in sand/silt areas, 1.0% of the remaining quahogs were found to be broken. There was no evidence of breakage of quahogs <60 mm valve length by the dredge, and there was no evidence that the dredge smothered quahogs by covering them with sediments. There was essentially no damage to quahogs directly by bullrakes, but handling of quahogs by bullrakers aboard the boat caused some breakage—0.1% to 0.3% of the total landed.

Estimates of Fishing Effort and Fishing Intensity

The number of fishermen in the quahog fishery and the average catch per fisherman are important data which can be useful for estimating fishing effort. The National Marine Fisheries Service (NMFS) makes annual estimates of the numbers of shellfishermen in Rhode Island. Based on the number of licenses issued and the number of boats registered to shellfishermen, NMFS estimates there to be between 1,000 and 1,300 full-time shellfishermen in recent years. This estimate is considerably higher than the estimate of 700-800 full-time shellfishermen currently used by Rhode Island Department of Environmental Management fisheries scientists (see Pratt et al., 1992 for discussion of estimation methods).

There have been two surveys of shellfishermen to gather data about the levels of fishing effort among shellfishermen. Holmsen (1966) and Holmsen and Horsley (1981) conducted mail surveys of all shellfish license holders and made estimates of the numbers of those deriving different proportions of their income from quahogging (Table 1).

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>none</td>
<td>139</td>
<td>113</td>
</tr>
<tr>
<td>less than 20%</td>
<td>359</td>
<td>297</td>
</tr>
<tr>
<td>about 25%</td>
<td>81</td>
<td>114</td>
</tr>
<tr>
<td>about 50%</td>
<td>65</td>
<td>135</td>
</tr>
<tr>
<td>about 75%</td>
<td>33</td>
<td>31</td>
</tr>
<tr>
<td>over 90%</td>
<td>138</td>
<td>338</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>815</strong></td>
<td><strong>1,028</strong></td>
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</tbody>
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Values in the table are expressed as a percentage of the total number of respondents (1,028).
The proportion of fishermen obtaining at least 75% of their income from quahogging increased from 21% to 36% in these two surveys. Holmsen (1966) also found an increase in full-time fishermen from the mid-1950s to 1961, indicating a trend of professionalization during periods of inclining as well as decreasing landings. One key conclusion of Holmsen's surveys is that one of the main characteristics of the Rhode Island quahog fishery is the relative ease of increasing or decreasing fishing effort as conditions change in the fishery or the general economy.

At present, the three commercial methods of quahogging in Rhode Island waters are with the use of tongs, bullrakes, and by commercial diving. Commercial diving has increased in importance as a method of quahog harvesting since the 1981 study of Holmsen and Horsley, so there is little information about the amount of fishing effort attributable to divers. Boyd (1991) provides an excellent historical overview of tonging and bullraking in Narragansett Bay. Over the years since the late 1940s, there has been a gradual shift in the use of gear from a predominance of tongs to a predominance of bullrakes.

The location of tong and bullrake fishing effort was mapped intermittently between June 1955 and August 1960 (Campbell and Dalpe 1960; Campbell, 1961). Maps generated by this project (Figure 8) showed that the major fishing effort was confined to the middle and upper Narragansett Bay, with tong fishermen confined to the shallower near-shore areas.

By use of a mail-survey questionnaire, Holmsen and Horsley (1981) showed similarly that most of the fishing effort was confined to the middle and upper Narragansett Bay (Figure 9). There is little published information about the location of fishing effort by shellfish divers.

Relative Gear Efficiencies and Environmental Impacts

There has been only one study in Narragansett Bay that compares the relative

Figure 8. Location of tong and bullrake fishermen in Narragansett Bay recorded between September 1959 and August 1960 (Campbell, 1961).

Figure 9. Percent of quahogging effort in selected areas of Narragansett Bay (Holmsen and Horsley, 1981).
impacts and efficiencies of different gear types (Glude and Landers, 1953). In this study carried out in 3-acre plots, the efficiency ratios for the bullrake and dredge were determined. The bullrakes used were able to most efficiently retain quahogs greater than 55 mm valve length, but some quahogs 35 to 55 mm in valve length were able to be retained. The dredge was able to most efficiently retain quahogs above 70 mm in valve length. There were no significant differences in the physical or biological composition of raked or dredged bottoms, but both had fewer living forms than the unfished control area. These authors concluded that there was no biological basis for prohibiting either bullraking or dredging.

A recent study on the environmental impact of bottom cultivation and removal of adult quahogs on the set and recruitment of quahogs was recently concluded (Sparsis et al., this volume). They found that after three months there were no significant differences in the physical, chemical, and biological parameters between fished, cultivated, and control plots because of high environmental variability.

Conclusions and Recommendations

There have been a considerable number of studies since 1946 focusing on the biology and fishery of quahogs in Narragansett Bay. The information base about the growth rates of quahogs in Narragansett Bay seems to be quite good. There appears to be a shortage of information about quahog recruitment. Some studies appear to indicate that there is a paucity of recruitment into some areas, yet there appears to be annual recruitment into other areas, particularly Greenwich Bay and upper Narragansett Bay. A systematic study of quahog recruitment patterns throughout Narragansett Bay is warranted. Estimates of fishing effort and fishing mortality in areas throughout Narragansett Bay are lacking, and much of the information that is available is now 10 years out-of-date. It is recommended that a socio-economic study similar to that of Holmsoen and Horsley (1981) be undertaken in order to update the fishing effort information. Additionally, given the current mix of harvest technologies, a study of the relative harvest efficiencies of tongs, bullrakes, and hand collecting by commercial divers is recommended. In conclusion, there is a great wealth of information available to fisheries managers about quahogs in Narragansett Bay. It is hoped that this review will provide a starting point for the assessment of where we have been in terms of the fisheries management studies, and that it will be useful in planning management strategies for Rhode Island's most important fishery resource.

References


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Game. Leaflet no. 1.


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Questions and Answers

Q. (Mr. John Finnern, shellfisherman) In the Glade and Landers study, were divers used to determine what was left and what was broken on the bottom?

A. (Dr. Michael Rice, URI) No, the Glade and Landers (1953) study used a large grab sampler that brought up intact sediments and quahogs after the dredging or bullraking treatments. Grab sampling can be used effectively for sampling because everything is brought up—juveniles, adults, etc. One possible problem with grab sampling is that care must be taken to avoid biases in breakage estimates, because some breakage will occur as the sampler hits bottom.

Subsamples from the center of the grab sample are representative of intact sediments. Grab sampling was used during the surveys of the 1950s and the Saila et al. (1965) study. More recent studies have used divers for sampling. Diving appears to be best for sampling juveniles and determining population structure without gear bias.

Indeed, the best way to calibrate sampling gear such as dredges, tongs, and rakes is by diver sampling.

Q. (Mr. George DeBlois, shellfisherman) You mentioned the Kassner and Malouf (1982) spawner transplant study in Great South Bay. What was the time frame of that study?

A. (Rice) Jeff Kassner, one of the people who did that work is in the audience. Perhaps he could answer that for you.

A. (Mr. Jeffrey Kassner, Brookhaven, New York) What that study did was to look at the spawning cycle of hard clams in the Great South Bay that was performed over a two-year spawning period. The underlying principal behind the spawner transplant was that broodstock were brought in from more northern, colder waters and had a retarded gametogenic cycle. The idea was to exploit the retarded cycle to extend the spawning period after the native stock had ceased spawning. What we found is that the natural spawning variability was so high that bringing in clams did not affect the recruitment. Additionally, bringing in 400 to 500 bushels did not make much difference when compared to the natural spawning stocks. Now the idea of spawner transplants evolved into the idea of spawner sanctuaries. If you then know the likely hydrographic larval dispersal patterns, you can strategically place your spawner stock for settlement in preselected areas.

Q. (Mr. Edgar Thompson) Are there any recent studies on the effects of pollution on quahogs? An example might be the effects of heavy metals on quahogs. There are a number of organizations such as Save The Bay that are committed to cleaning up the Bay, and I want to know if there has been some headway.

A. (Rice) There are a considerable number of studies on this. In the first quahog conference we held in 1990, Ms. Katrina Kipp of the Environmental Protection Agency and the Narragansett Bay Project gave a very excellent review of studies of Narragansett Bay in which quahogs were analyzed for heavy metals, various organic
pollutants, and pesticides. She outlined the risk assessment program in which the health risk to people eating Narragansett Bay quahogs was compared to other common health risks. In general, Narragansett Bay quahogs carried a rather low-risk value to the consuming public. Sheldon Pratt from here at GSO had one study that looked at quahog populations in the Providence River, and the adults are alive and well. One interesting study that came out of the National Marine Fisheries Service shellfish lab in Milford, Connecticut showed that heavy metal pollutants are much more toxic to bivalve larvae than they are to adults. It is possible that shellfisheries in polluted areas might be damaged by reducing recruitment rather than by the outright killing of adults.

Q. (Johnson) In a nutshell, do you believe that we are moving forward or backward.
A. (Rice) Well, I think we're probably moving forward. Improvements in upper Narragansett Bay water quality due to the improvements by the Narragansett Bay Commission to the combined sewer overflow system are a positive step forward. Shellfish openings (albeit not all the time) in the conditional areas suggest some improvement. The next thing in line, however, is the nonpoint source pollution problem. This is a much more expensive problem, and technically a harder nut to crack.

Q. (Mr. David Borden, DEM) You have summarized where there is knowledge and where there is need for more work. Can you give me some sense of priority on what studies you think are most important?
A. (Rice) As it so happens, we have a full panel discussion this afternoon, with your question as our topic. So, please stay tuned.

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