A review of the factors influencing the growth of the northern quahog, Mercenaria mercenaria (Linnaeus, 1758)

Michael A Rice, University of Rhode Island
Jan A Pechenik, Tufts University

Available at: https://works.bepress.com/michael_rice/28/
A REVIEW OF THE FACTORS INFLUENCING THE GROWTH OF THE NORTHERN QUAHOG, _MERCIERA MERCIERIA_ (LINNAEUS, 1758)*

MICHAIL A. RICE¹ AND JAN A. PECHENIK²
¹Dept of Fisheries, Animal and Veterinary Science
The University of Rhode Island
Kingston, Rhode Island 02881 USA
²Dept of Biology
Tufts University
Medford, Massachusetts 02155 USA

ABSTRACT Factors affecting the growth of larval, juvenile, and adult northern quahogs, _Mercenaria mercenaria_, are reviewed. Larval growth is affected by temperature, salinity, current speed, dissolved oxygen concentration, and the amount of suspended sediments in the water, along with such nutritional factors as food quantity and quality. Growth of post-set juvenile and adult quahogs is similarly affected by the same physical and nutritional factors. Recent work suggests that there is a strong genetic contribution to quahog growth rate and that selective breeding programs may be useful for producing rapid growth strains. A growing body of evidence suggests that larval growth rates are poor predictors of post-set juvenile growth rates. Indeed, preliminary evidence suggests that shorter larval development periods correspond with higher rates of growth in post-set animals. Further research into this aspect of the developmental biology of quahogs is recommended.

KEY WORDS: quahog, _Mercenaria_, growth, development, larvae, juveniles

INTRODUCTION

With the long-standing interest in fisheries management of the quahog, _Mercenaria mercenaria_, there has been considerable work aimed at elucidating the factors affecting recruitment into the fishery and the subsequent growth rates of recruited juveniles, especially at the population level. The biology of larval and juvenile stages tends to be studied separately. A number of workers have examined the role of temperature, diet, and other environmental factors on larval survival and growth (reviewed by Pechenik, 1987). Traditionally, studies on juveniles have focused on the role of such physical factors as temperature, salinity, current speed, and substrate composition on quahog growth. With the increasing interest in commercial quahog culture, nutritional factors such as food quantity and quality have been a major focus. More recently, a number of culturists have begun focusing on the heritability of juvenile growth rates. The possible contribution of larval biology to juvenile growth has been much less studied.

Few studies have been undertaken to determine the possible interaction between rates of larval and juvenile development, and the extent to which larval biology and larval culture conditions may influence juvenile growth rates. It is generally recognized that larvae accumulate nutrients to fuel successful metamorphosis, but pre- and post-metamorphic quahogs feed using very different mechanisms. There is no a priori reason to believe that fast growing larvae will necessarily grow more rapidly than fast-growing juveniles. Alternatively, larval growth rate may not be the best indicator of overall development rate. In this paper, we review the factors known to influence the growth of both larval and juvenile quahogs, and identify some areas in which additional studies may be warranted.

*This work was supported in part by the Rhode Island Agricultural Experiment station project number M-440. This is publication number 2774 of the College of Resource Development, The University of Rhode Island.
larvae did not develop beyond the trochophore stage. Quahog larvae stopped growing when dissolved oxygen was reduced to 2.4 mg O₂/L or below, but resumed growth once normal oxygen concentrations were restored. Larvae grew most rapidly when dissolved oxygen concentrations were at least 4.2 mg O₂/L.

Effects of Particulate Inorganic Matter

A number of experiments performed at the Milford Laboratory have shown that suspended sediments may inhibit larval growth, although effects varied markedly with the type of material in suspension (Davis 1969, Davis and Hida 1969). Larval growth rate was inhibited at concentrations of 250 mg/L chalk and 500 mg/L clay and Fuller's earth. In contrast, quahog embryos and larvae grew and developed normally in concentrations of natural silts up to 750 mg/L. Larval growth rate was reduced in 1 g/L silt, and larvae did not grow at all at concentrations above 2 mg/L silt. Although quahog larvae can reject particulate inorganic matter (PIM) at low concentrations of suspended material, they lose this ability at higher PIM concentrations. This leads to the ingestion of PIM and subsequent deleterious effects on growth.

Effects of Nutrition

From the earliest days of bivalve mollusk hatcheries, phytoplankton has been cultured as feed for larvae and for broodstock in their conditioning for spawning (Wells 1928; Loosanoff and Davis 1930, Loosanoff 1951). With the desire to optimize hatchery production of quahogs, a number of studies have been undertaken to quantify filtration rates on particular diets (e.g., Rijksyard 1988) and to assess the nutritive value of various phytoplankton species for quahogs. Davis and Galliard (1958) and Walne (1970) compared the food value of several species of phytoplankton by monitoring larval growth (μm shell growth/day). Phytoplankton which were able to sustain rapid growth in quahogs included: Isochrysis galbana, Dicystosoma inornata, Pavlova (Monochrysea) ultheri, Tetraselmis suecica, Thalassiosira pseudonana, Skeletonema costatum, and Chaetoceros calmarum. There is considerable evidence that mixtures of two or more good quality algal species will allow much faster growth of quahogs than any single phytoplankton species alone (Walne 1974, Epifanio 1976, Epifanio 1979a). One drawback with the use of cultured phytoplankton is that their nutritional value may vary with culture conditions (Wickfors 1986, Thompson et al. 1990), and may subsequently affect larval or juvenile growth (Wickfors et al. 1984, Whyte et al. 1990). A secondary drawback with algal diets is that in commercial aquaculture applications, production of algal foods for larval and juvenile bivalves can represent a major fraction of the total production costs. Walsh et al. (1987) estimated that the production of algae at the Aquacultural Research Corporation hatchery in Dennis, Massachusetts to be $250/kg dry weight. To lower production costs and standardize food quality, efforts have been taken to develop artificial (non-algal) diets for bivalve larvae and juveniles. Although some non-algal food supplements have been used for rearing bivalves (e.g., Haven 1965), there has been very little progress toward a nutritionally complete artificial diet for bivalve larvae (Epifanio 1979b, 1982). Urban and Langdon 1984, Courteau and Sorensen 1992). Langdon (1983) used the technique of microcapsulation of nutrients as the basis of his artificial diet, but the growth of larvae was only about 20% of his algal-fed controls. The reasons for this slow progress in developing an artificial diet include the difficulty of determining the specific nutritional requirements of bivalve larvae, the digestibility of potential food items, and the leaching of water soluble nutrients from particles in the optimum 3 to 35 μm size range (Webb and Chu 1982, Langdon and Siegfried 1984).

Environmental Influences on Juvenile and Adult Growth Rates

Effects of Temperature

Growth of post-metamorphic juvenile and adult quahogs is greatly affected by temperature. Ansell (1968) reviewed the growth of quahogs in various locations along the eastern coast of the United States, and concluded that the optimum temperature for shell growth was about 20°C and that shell growth ceased below 9°C or above 31°C. There was little evidence that the relationship between temperature and quahog growth rate differed throughout its geographical range.

In his study of the effects of temperature on quahog growth, Ansell (1968) compared growth of animals of roughly the same age. Comparisons of growth rate between juvenile quahogs and older, larger individuals can be problematic. This is because most organisms, including bivalves, experience an ontogenic decline in growth rate (e.g., Reiss 1989). Typically, growth rates of biological organisms are described by a negative exponential function that reaches an asymptotic value. By using a technique of fitting empirical growth data to various negative exponential functions (Kofman 1981), Jones et al. (1989) concluded that quahog growth is best described by the von Bertalanffy (1938) growth function. Of course, if one were simply making short-term measurements of juvenile growth, simple measurements of size attained per unit time are adequate in most instances. However, for long-term growth studies or analysis of field populations, the von Bertalanffy growth function is most appropriate. With adequate care (Knight 1968; Appleford 1983), the Bertalanffy growth model can be used to compare differences in growth between quahog populations and to deduce effects of temperature and other physical and biological factors on growth.

Ansell (1968) used shell growth as the key criterion for growth, but Peterson and Fegley (1986) suggested that shell growth is not the only criterion by which growth can be assessed. Growth of soft tissues is not necessarily coupled to shell growth at all times of the year. Peterson and Fegley showed that even after correction for ontogenetic growth rate differences, adult quahogs in North Carolina have anomalously lower growth rates during winter months in relation to juveniles. They interpreted this as differences in energy and nutrient reserve partitioning prior to the spring burst of gametogenic activity (Loosanoff 1937). Although there may be these differences in resource partitioning between soft tissues and the shell on a month-to-month basis, average annual growth is reflected in shell growth patterns. Using this as the basis of their study, Jones et al. (1989) showed that there is a high degree of correlation (r = 0.88) between mean annual growth of quahogs in Narragansett Bay and mean annual water temperature.

Effects of Salinity

In comparison to temperature, changes in salinity do not have a major influence on growth rates. In most instances quahog juveniles and adults grow fastest when salinities exceed 20 ppt (Casagrande and Krausser 1981), and growth is reported to be optimal between about 26 and 27 ppt (Davis, n.d.).
Factors Affecting Growth of Northern Quahog

Effects of Substrate

A number of studies have shown that shell growth of juvenile or adult quahogs is 19% to 30% greater in predominantly sandy sediments as compared to muds (silt-clay sediments) (Pratt 1933, Pratt and Campbell 1936, Richards and Pinella 1970). More recent work (Grizzle and Morris 1989, Grizzle and Lutz 1989) employed an experimental protocol to compare the relative effects of sediment type, current speed and seagrass concentration. The results suggested that although there was an influence of sediment type on quahog growth, they were more similar in comparison to the effects of current velocity and seagrass concentration. The increased growth associated with sandier sediments in the earlier studies has been interpreted to be a secondary result of smaller sediments being associated with higher current regimes.

Effects of Food Quantity and Current Speed

The rates at which quahogs feed on various phytoplankton species have been determined in static culture systems (e.g., Rice and Smith 1958, WaIe 1972). In Welch’s (1972) study, quahogs with valve lengths of 4 to 5 mm had maximum filtration rates of 3.4X10^-2 cells/hr for Isochrysis galbana and 9.8X10^-2 cells/hr for Phaeodactylum tricornutum. Efforts have been made to relate rates of filter feeding with quahog growth (e.g., Golstein and Roels 1980). Food filtration rate and growth determinations of this type are useful only in the specialized case of rearing animals in static systems. In most modern nursery and growout systems, as well as in the wild, food is delivered to quahogs via water currents and phytoplankton concentrations are typically three to four orders of magnitude lower in concentration than in the static rearing systems. Recognizing this recent studies have sought to determine quahog filtration rates at environmentally realistic phytoplankton concentrations and current regimes (e.g., Heithert 1977, Dorin and Ovian 1986, Judge et al. 1992b).

Since the pioneering work of Kellogg (1952), it has been recognized that current speed has a major stimulatory effect on the growth of quahogs. Subsequent researchers (Kerstwell 1949, Haskin 1952, Hadley and Manzi 1984, Manzi et al. 1985) have also reported this relationship and have explained it as a result of increased food (seston) supply rate in higher current regimes. The works by Grizzle and Morris (1989) and Grizzle and Lutz (1989) strongly suggest that quahog growth is primarily determined by horizontal seston flux (the product of seston concentration and current speed) past the animals. Quahogs in very dense assemblages (>100 adults/m^2) grow more slowly than do individuals in less dense assemblages, suggesting that food-limited starving can occur in nature (Peterson and Bea 1989, Rice et al. 1989) as well as in grow out culture systems (Zibigdige et al. 1979, Evervole et al. 1990). Recently, Judge et al. (1992a) performed a field experiment in which quahogs were placed in a series of artificial channels designed to vary current speeds, yet allow all quahogs to be exposed to the same ambient seston concentrations. This protocol allowed for discriminating between growth effects due to water flow and effects due to food availability. Under conditions of adequate food supply (food-limited growth not a factor), a doubling of current speed (up to 27 cm/sec) had no effect on growth rate. So current speed alone in the 10 to 27 cm/sec range does not in itself affect growth, but only serves to replenish food locally depleted by the actively filtering bivalves.

Although most researchers have concluded that quahog growth and current speed are positively correlated, there are some circumstances in which this general rule does not hold true. One study suggests that quahog growth can be inhibited in sandy sediments with very high current speeds and in silty areas where current surges may resuspend sediments, leading to decreased nutritive value of available particulates (Murphy 1985). In other studies, increased growth was noted in quahogs in seagrass beds (Peterson et al. 1984, Ireland and Peterson 1991), yet overall current speeds were much less in the seagrass than in adjacent areas without seagrass. These surprising results are explainable by the observation that seagrass beds contain much higher food concentrations than in adjacent non-seagrass areas (Judge et al. 1992b). Although current speeds are lower, quahog growth remains high because of the localized productivity within the seagrass, and possibly because of 'hydrodynamic trapping' of particulates by the low flow rates in the sea grass (e.g., Eckman 1990).

Effects of Food Quality

Unlike the example of quahogs in artificial culture situations, quahogs in the wild are frequently faced with less than optimum food quality. For example, WaIe (1970) noted that some species of phytoplankton such as Nannochloris atomas and Phaeodarcylum tricornutum were very poor food organisms for quahogs. A series of experiments outlined by Epifano (1982) showed that it is unlikely that slow growth of quahogs led Phaeodactylum tricornutum could be attributed to a toxic algal metabolite, but the amino acid profile and other nutrient levels appeared adequate to support growth of quahogs. The conclusion was that for some reason, quahogs have difficulty digesting P. tricornutum. Nannochloris atomas is often found during the warm summer months in estuaries which receive nitrogen and phosphate enriched effluents (Mitchell-lane 1973). Bass (1983) and Bass et al. (1990) demonstrated that cells of this phytoplankton species pass through the gut of quahogs almost completely undigested, which may explain the reduced quahog growth observed in areas characterized by persistent summer blooms of N. atomas.

In addition to the question of food quality and digestibility, there is some evidence that various phytoplankton species produce toxins that adversely affect bivalve feeding, and ultimately growth. For example, due to toxins associated with the brown tide organism Aureococcus anophagefferens, blue mussels Mytilus edulis ceased feeding, resulting in reduced growth and elevated mortality (Tracey et al. 1988). It seems likely that A. anophagefferens can similarly interfere with suspension feeding by quahogs (Draper et al. 1990). The dinoflagellate Alexandrium (Protoceratium) tamarense causes quahogs to exhibit pronounced valve closure and a reduction of feeding rate (Shumway and Cacil 1987). Recent work by Wickfors and Smolowitz (1992) similarly suggests that toxins associated with blooms of the dinoflagellate Proceratium minimum can interfere with quahog growth.

Effects of Particulate Inorganic Matter on Feeding and Growth

Since the work of Rice and Smith (1958), it has been known that substantial concentrations of silt can lower the filtration rates of juvenile and adult quahogs. More recently, Britzel and Malouf (1984) showed that although silt concentration below 5 mg/L had no effect on filtration rate, concentrations between 20 mg/L and 40 mg/L reduced particle filtration rate by 31% and 52% respectively. This reduction in filtration rate may impair food acquisition and overall nutritional state of quahogs. Britzel et al. (1984) found no effect on shell growth of juvenile quahogs in silt levels up to 44...
mg/L. Soft tissue growth was not affected at 25 mg/L, but was reduced by 16% in 44 mg/L. Murphy (1985) noted decreased shell growth in quahogs from areas of high suspended silt. In a recent study, Turner and Miller (1991) found that filtration rates and shell growth of quahogs were depressed in simulated storm events in which suspended sediment levels reached 193 mg/L.

Although silt or particulate inorganic matter (PIM) is known to reduce juvenile and adult filtration rates, the mechanisms of particle sorting and pseudofeces formation can compensate for the reduction of total filtered particles and allow for ingestion of high quality food particles. Breit and Malouf (1984) found that the threshold for pseudofeces production was 10 mg/L total silt (particulate). Sorting of particulates by the labeled paupers resulted in 78% retention of algae and >70% rejection of PIM. In circumstances where there are mixtures of phytoplankton and PIM, some of the PIM is ingested. In low to moderate suspended silt concentrations, there may actually be an increase in growth rates. This phenomenon has been attributed to a possible abrasive effect of the silt in disrupting algal cells as they pass through the digestive tract, particularly the style sac (Reid 1982).

**Influence of Genetic Factors on Quahog Growth**

With the growing interest in quahog aquaculture, there has been an interest in selective breeding programs to enhance growth potential and other commercially desirable characteristics of hatchery stocks (see reviews by Newkirk 1980, 1983). The rate at which juvenile bivalve mollusks grow can be considered one component of fitness, since the primary mechanism by which juvenile quahogs escape size-selective predation and smothering by sedimentation is through growth (MacKenzie 1977, Blunden and Kennedy 1982, Boulding and Hey 1984, Rawson and Hibbush, 1990). Additionally, the age at which quahogs become sexually mature and the total reproductive output correlate strongly with size (Breit and Malouf 1983, Byne and Neves 1983, Peterson 1986). Thus individuals showing the most rapid juvenile growth are likely to have greater lifetime reproductive success. Because of these selective pressures one would expect that there would be a chronic selection for high growth rates and low levels of heritable variation (Moiseau and Roff 1987, Rawson and Hibbush 1990). Yet many studies of juvenile quahog growth under optimal environmental conditions show very high levels of growth variation (e.g. Eldridge et al. 1979, Eversole et al. 1986, Malaowski 1985, Littlefield 1991). A study by Rawson and Hibbush (1990) suggests that genetic variability of quahog growth may be maintained despite selective pressures because its planktotrophic larval dispersal will distribute siblings over a wide range of environments where genetic variation in growth may be differentially expressed. This genotype-environment interaction may act to maintain high levels of genetic variation in any particular locale (see Via and Lande 1987, Gillespie and Turell 1989 for discussion of genotype-environment interactions). Rawson and Hibbush (1990) concluded that there is sufficient genetic variability among quahogs so that selective breeding programs can be useful for producing high-growth strains.

A number of studies have been undertaken to explain the genetic component of growth rate variability among individual bivalves. Hibbush et al. (1992) have demonstrated that most of the variation in larval growth rate is heritable in the quahog M. mercenaria. Also, significant correlations between multiple locus heterozygosity at various enzyme coding genes and growth rate have been found in a number of bivalves in field populations, including the mussel Mytilus edulis (Koehn and Gaggenau 1964), the oyster Crassostrea virginica (Zouros et al. 1980), and the cockle clam Musiula lateralis (Gorten et al. 1984). Such correlations suggest that dominance interactions at some gene loci may be responsible for bivalve growth variation, but this relationship has been much less clear in hatchery and nursery studies. Hatchery studies of oysters (Foltz and Chlutt, 1986) and quahogs (Adamkiewicz et al. 1984) have failed to show a significant correlation between growth and isozyme heterozygosity. Recent evidence suggests that quahogs from stable natural environments can exhibit a lack of correlation between growth and degree of heterozygosity (Shattrey et al. 1991). Citing several other similar studies as well as their own data, Gaffney and Scott (1984) showed that there may be a linkage disequilibrium between enzyme marker loci and the loci affecting growth in hatchery stock, and expressed strong skepticism about relying on heterozygosity being an adequate tool for molluskan breeding programs aimed at growth enhancement. Dillon and Manzi (1988) provide evidence that the phenomenon of linkage disequilibrium may occur in hatchery/nursery stocks of quahogs. This linkage disequilibrium between growth and heterozygosity has been recently exploited by Manzi et al. (1991) who showed that reciprocal crosses between growth selected hatchery stocks can be useful for increasing or maintaining genetic variability without loss of rapid growth traits.

**Relationships Between Rates of Larval and Juvenile Growth**

Although a substantial fraction of the variation in the growth rate of bivalves is genetically determined, there is a growing body of evidence that the correlation between larval growth rates and the growth rates of juveniles may be very poor. This is in spite of the fact that it is common hatchery practice to call slower growing larvae (e.g. Dupuy et al. 1977, Castigna and Kraemer 1981). Poor correlations were found between larval and juvenile growth rates for the oysters Crassostrea gigas (Lannan 1972), Crassostrea virginica (Loeze 1979), and Ostrea edulis (Newkirk and Hale 1983) and for the mussel Mytilus edulis (Springman and Nielsen 1989). Similar studies with the gastropod Crepidula fornicata also suggest that individual larval growth rates may be poor predictors of individual post-metamorphic growth rates (Pechenik et al. 1987 and unpubl. data). More recently, Heffernan et al. (1991) found that quahog larvae produced by adults selected for rapid post-metamorphic growth grew significantly (p < 0.01) more slowly than did those produced by control populations. The implication is that slower-growing larvae may give rise to faster-growing adults, although that possibility has not yet been assessed directly. These data suggest that the routine culling of small larvae in standard hatchery practice may be removing those individuals that are likely to grow to market size most quickly following their metamorphosis (Heffernan et al. 1991, 1992). As emphasized recently by Hibbush et al. (in press), this apparent lack of correspondence between larval and adult growth rate probably reflects shifts in the expression of those genes associated with feeding and digestive processes during development.

Growth of juvenile bivalves may be better predicted by aspects of larval development other than larval shell growth rate. Growth is but one component of development, typically reflecting increases in cell numbers; differentiation is another component of development—a less commonly studied component—that reflects coordinated shifts in gene expression (discussed by Pechenik,
FACTORS AFFECTING GROWTH OF NORTHERN QUAHOG

1987, p. 569, Pechenik et al., 1950). Rates of mollusc growth and differentiation are not necessarily well coupled. For example, Pechenik et al. (1950) found that the gills of mussel larvae (Mytilus edulis) at different temperatures dramatically altered the relationship between individual shell growth rate and the amount of time required for larvae to develop "eye-spots."

Two little-studied components of development that may influence juvenile growth are (1) the time required for individual larvae to become competent to metamorphose and (2) the amount of time that larvae delay their metamorphosis before they finally metamorphose, as discussed in the next section.

Competence, Delayed, Metamorphosis, and Correlations with Growth

Bivalve larvae typically do not develop for a time in the plankton before they become capable of metamorphosing (reviewed by Pechenik 1985, 1990). We presently have a poor understanding of what makes an individual competent to metamorphose. Likely candidates include the construction and activation of certain epidermal sensory receptors, the completion of specific nervous system systems, the activation of chemical receptors on target tissues, or the development of competence of key neural pathways (Hadfield 1978, Travis-Plowman and Morse 1986, You et al. 1986, Pechenik and Heyman 1987, Todd et al. 1991, Pechenik and Gec, in press).

None of these mechanisms are directly related to larval growth rate. Indeed, Zimmerman and Pechenik (1991) have demonstrated for the marine gastropod Crepidula plana that the relationship between larval growth rate and time required for larvae to become metamorphically competent can be altered dramatically by shifts in ambient temperature and salinity; time to competence was poorly predicted by relative larval growth rate in their experiments.

Whatever the mechanism, the possibility that individuals that become competent to metamorphose sooner give rise to juveniles with higher fitness has not been examined. However, preliminary data presented by Newkirk et al. (1977) and by Losse (1979) suggest that for the oyster C. virginica, shorter time to metamorphosis correlates with higher juvenile growth rates. Additional studies examining the relationships between larval growth rate, time to competence, and post-metamorphic growth rate seem warranted.

Once a larva becomes competent—but not before—metamorphosis can generally be triggered by contact with certain chemical or physical environmental cues (reviewed by Thorson 1958, Gips 1974, Shulke 1974, Burke 1983, Hadfield 1984). Larvae of the oysters Crassostrea virginica and C. gigas, for example, are induced to metamorphose by certain bacterial films and (and sometimes of those films) (Fitt et al. 1989, Weisser et al. 1989) and mussels Mytilus chilensis are induced to metamorphose by the presence of byssal adhesive disks (Padilla 1989). In the absence of such cues, larvae delay their metamorphosis and continue to swim (reviewed by Pechenik 1990). As metamorphosis is delayed, the threshold stimulus required to induce metamorphosis typically declines, so that larvae may become less discriminating with time and eventually attach and metamorphose on substrates that were unreactive to newly competent individuals (Scheelmann 1961, Knight-Jones 1953, Gips 1988, Coen et al. 1990, Pitt and Coen 1992).

Larvae that metamorphose on the plastic or resin walls of culture tanks or on other artificial substrates provided in bivalve hatcheries may have become competent to metamorphose much earlier in development. There is evidence from invertebrate phyla that fitness may decline during delayed metamorphosis, depressing juvenile growth and/or survival (Morse et al. 1979, Highsmith and Emlet 1986, Woollacott et al. 1989, Pechenik and Cerulli 1991, Pechenik et al. in press). Few women have investigated this phenomenon in bivalves, but a gradual physical degeneration of mussel Mytilus edulis larvae delaying metamorphosis has been described by Haynes 1965, suggesting that post-metamorphic survival and growth may be compromised. The potential impact of delayed metamorphosis on the growth and survivorship of juvenile quahogs seems worthy of study.

SUMMARY AND CONCLUSIONS

The physical and nutritional factors affecting the growth of larval, juvenile and adult quahogs have been studied since the turn of the 20th century. Key environmental factors affecting quahog growth include temperature, salinity, current regime, and concentration of suspended sediments. Nutritional factors affecting quahog growth include the quantity and quality of particulate foods, especially phytoplankton. Considerable work has been aimed at developing nutritionally complete, non-algal diets for larvae and juveniles but this is progressing slowly and may deserve further attention. Recent efforts to improve hatchery stocks of quahogs has led to a growing understanding of the genetic factors determining growth. Evidence suggests that there is sufficient heritable variability among quahogs to permit selection breeding programs to produce high growth strains.

However, much of the work involving environmental, nutritional and genetic determinants of quahog growth have focused on either larvae or post-set animals. Recent work with various bivalve species in which both larval and post-set growth are monitored in the same experimental protocol has shown that larval and juvenile growth rates are often poorly correlated. Some preliminary evidence suggests that juvenile growth rates may be better correlated with brevity of the larval developmental period than with rapidity of larval growth. Moreover, there is a reason to suspect that post-metamorphic growth rate or survival may be enhanced by promoting metamorphosis shortly after larvae become metamorphically competent. These aspects of quahog developmental biology and their correlation with quahog growth deserve further attention because of both practical and academic implications.

LITERATURE CITED

Factors Affecting Growth of Northern Quahog


Factors Affecting Growth of Northern Quahog


