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Distribution of Quahog Larvae Along a North-South Transect in Narragansett Bay

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DISTRIBUTION OF QUAHOG LARVAE
ALONG A NORTH - SOUTH TRANSECT
IN NARRAGANSETT BAY

BY

NURLISA A. BUTET

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
FISHERIES, ANIMAL, AND VETERINARY SCIENCE

UNIVERSITY OF RHODE ISLAND

1997

MASTER OF SCIENCE THESIS

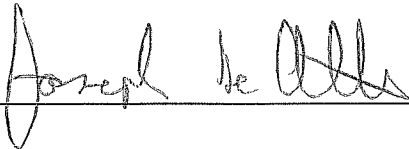
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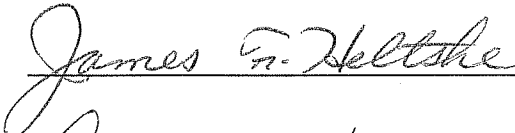
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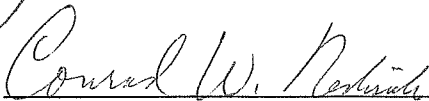
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1997

ABSTRACT

A study on the distribution of quahog (*Mercenaria mercenaria* (Linnaeus 1758)) larvae in Narragansett Bay, Rhode Island was conducted during a single summer season in 1995. Samples of the larvae were collected weekly using an electric bilge pump and a 60 μm mesh plankton net at two depths (0.3 m and 1.6 m) at five sampling stations distributed landward along the West shore, 12.6 km to 30.6 km from Rhode Island Sound. Three stations were located in the upper estuary, i.e., Upper Bay, and two stations were in the lower estuary, i.e., Upper West Passage.

The temporal distribution of quahog larvae was consistent with moon phase; more larvae were found during neap tides. Early stage larvae, i.e., D-hinge veligers at the age of 1-3 days occurred weekly throughout the period of sample collection and reached peak abundance on June 20. In contrast to the constant occurrence of early stage larvae, late stage larvae, i.e., umbonate veligers, were sometimes absent in the plankton samples. The late stage larvae reached peak abundance on July 7 at all but one station. On the basis of the peak abundances of the two developmental stages, I confirm that the duration of planktonic life of quahog larvae is about 2-3 weeks. Due to high abundances of late stage larvae during this period, the highest intensity of settlement probably occurs in Narragansett Bay around mid July. There was a tendency for a different distributional pattern between the larvae collected from Upper Bay and Upper West Passage stations.

Densities of quahog larvae decreased away from the major spawner stock area (Providence River) probably due to the effect of tidal and non-tidal currents and turbulent diffusion. Tidal excursions of 1 - 4.4 km could be responsible for displacing the larvae from the Providence River into as far as Upper Bay in one

ebb tide. It is probable that small numbers of larvae might be transported into Upper West Passage due to non-tidal currents. It appears that Upper Bay stations are the areas with relatively higher larval retention than other parts of the Bay.

Multiple linear regression analysis indicated that only 20 % of the total variability of quahog larval densities in Narragansett Bay is explained by the independent variables, i.e., sampling depths, moon phase, water temperature and station location.

ACKNOWLEDGMENTS

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I must express my deep appreciation for the support of my friends : Neil Thompson for helping me with sample collection and teaching me to operate the Boston Whaler, and Joe Goncalo for sharing his thoughts on the identification of the bivalve larvae.

This study would not have been accomplished without the financial support from Environmental Study Center - Development Project of the Government of the Republic of Indonesia.

My special gratitude to my husband for his love and support which kept me going.

Finally, I dedicate this work to my late parents who kept encouraging me to study.

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INTRODUCTION

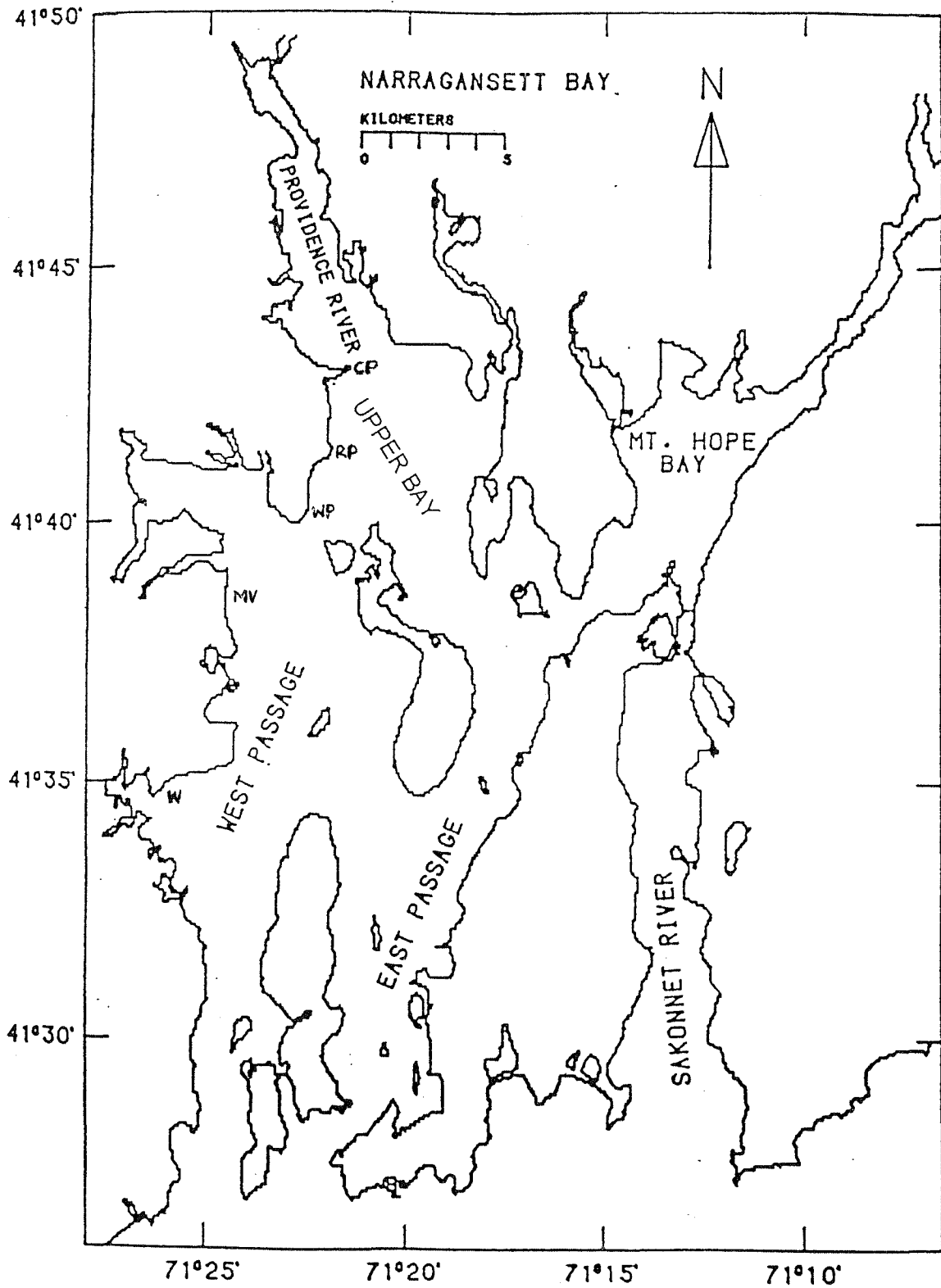
Statement of Problem

The quahog (*Mercenaria mercenaria*) fishery in Rhode Island is of major economic importance. It is considered to be the largest inshore fishery within the state (Pratt, 1988; Lazar et al., 1995). The fishery began in pre-colonial times (Rice, 1996), and has gradually become more important following the decline of the oyster fishery between 1930s and 1950s, primarily due to pollution (Pratt, 1988; Bean, 1990). The commercial landings of quahogs depend almost entirely upon the stock in Narragansett Bay (Lazar et al., 1995; Rice and Goncalo, 1995), the principal estuary in the state of Rhode Island. The harvest reached a peak of 5 million pounds in 1955, after which catch declined (Lazar et al., 1995). A second peak of 4 million pounds occurred in 1983. However, commercial landings in 1994 ranked second to Connecticut among other states in New England (Rice, 1996).

The harvestable quahog stocks in Narragansett Bay are not distributed uniformly (Pratt, 1988). There is a tendency of decreasing numbers from upper to lower estuary (Pratt, 1988). In the upper estuary, the Providence River area and Upper Bay (Figure 1), which are prohibited areas for shellfishing (Bean, 1990), have the highest densities of adult quahogs, and these quahogs constitute a potential spawning stock (Pratt, 1988). In contrast, the West Passage in the lower estuary, an open area for shellfishing (Bean, 1990) has a much lower quahog density (Rice, 1993).

Despite many studies focusing on the adult quahog populations (Stickney and Stringer, 1957; Salla et al., 1967; Jones et al., 1989; Rice et al., 1989), there have been few studies on quahog larvae in Narragansett Bay. Landers (1954)

Figure 1. Map of Narragansett Bay showing five sampling stations.
CP, Conimicut Pt.; RP, Rocky Pt.; WP, Warwick Pt.; MV, Mt. View;
W, Wickford.



studied the abundance of bivalve larvae - assuming them to be quahog - during three consecutive years (1950, 1951, and 1952) at two Narragansett Bay sites, in Greenwich Bay and off Wickford (Figure 1). No other study directed attention at the distribution of bivalve larvae in Narragansett Bay for about 40 years, until Rice and Goncalo in 1993 conducted their study at seven stations in Greenwich Bay. Therefore, to establish a better understanding of the ecology of early life stages of quahogs, this study attempts to describe patterns of quahog larval distribution in the western part of Narragansett Bay.

Literature Review

The northern quahog is a filter feeder inhabiting shallow coastal waters from the Gulf of St. Lawrence in Canada to Florida (Rice, 1992). Like many other bivalves, young quahogs are typically males. In successive years they may change sex and produce eggs, a characteristic called protandric hermaphroditism (Rice, 1992). Both eggs and sperm of adults are expelled in the water column, thus, fertilization proceeds externally (Rice, 1992). Spawning normally begins in the late spring as water temperature increases (Menzel, 1989; Rice, 1992), and it lasts into the summer months (Bricelj, 1993; Rice 1993). Therefore, the existence of the larvae of quahog in the water column is considered temperature - dependent.

Larval quahogs pass through a series of well-defined, recognizable stages characterized by appearance and dimension (Carriker, 1961; Loosanoff et al., 1966; Chanley and Andrews, 1971). According to Carriker (1961), by 12 hours after fertilization, a fertilized egg becomes a planktonic trochophore larva. The shape of this larva is oval; it has a dense mat of long cilia over the equatorial region. At an age of 1 - 3 days, a velum develops to facilitate

swimming. At this stage, a 90 - 140 μm straight-hinge is formed at the dorsal section of the valves. Thus, it is called a straight-hinged veliger or early stage larva. At a valve length of 140 - 220 μm , or at an age as early as three days, the larva develops into an umbonate stage or late stage larva in which the umbo rises slightly above the hinge line. At six days the larva develops a foot and enters pediveliger stage where the valve length is 170 - 220 μm ; the velum is still present. Both foot and velum facilitate finding a suitable substrate for settlement and metamorphosis.

Early stage bivalve larvae in St. Mary's River, Maryland (Manning and Whaley, 1954) and Greenwich Bay, Rhode Island (Rice and Goncalo, 1995) tended to remain in the upper water column, while late stage larvae stayed close to or on the bottom. The difference in depth distribution may be a function of stage - dependent specific gravity of the larvae. Younger larvae have lower specific gravity than seawater; the specific gravity of the older larvae is greater (Manning and Whaley, 1954). Rice and Goncalo (1995) speculated that the effect of light was responsible for depth distribution; early stage larvae were considered positively phototactic as they occurred near the surface, while late stage larvae were considered negatively phototactic because they occurred away from the surface.

According to Wood and Hargis (1971) the selective swimming process (i.e., sinking and rising throughout the tidal cycle) within the water column is stimulated by tides. The late stage bivalve larvae in a New Jersey estuary dropped on or close to the bottom during the period of slack water and remained there through the falling salinities of ebbing tide. They were apparently stimulated to rise by the increasing salinity of early flooding tides (Carriker, 1951). In contrast, early stage larvae showed uniform vertical distribution throughout the tidal current cycle (Carriker, 1951; Kunkle, 1958).

The ability of bivalve larvae to adjust their position vertically in the water column may provide the most important mechanism in controlling horizontal distribution (Ketchum, 1955; Kunkle, 1958; Wood and Hargis, 1971; Okubo, 1994; Samarco and Heron, 1994) and, ultimately, their recruitment success (McConaugha, 1988). Their horizontal displacement, like many other species having planktonic larvae, is subject to estuarine circulation (Sandifer, 1975) induced by tides (Carriker, 1955; Kunkle, 1958; Carriker, 1961; Seliger et al., 1982; Andrews, 1983), gravitational circulation (Ketchum, 1954; Wood and Hargis, 1971; Okubo, 1994), and wind (Manning and Whaley, 1954).

Larvae inhabiting upper water column during ebb tides can be dispersed seaward, and the densities were lower than those during flood tides (Carriker, 1961; Andrews, 1983). Nelson (1955) studied the distribution of oyster larvae in Barnegat Bay, New Jersey and found that the early stage larvae were carried as far as 3.4 km seaward from spawning beds. In order to maintain their existence in the estuary, the larvae should, therefore, swim bottomward during ebb tides as lower layer gravitational circulation may carry the larvae landward (Wood and Hargis, 1971; Sandifer, 1975).

On the studies of oyster larvae near Oösterschelde, Holland (Korringa, 1947) and quahog larvae in Little Egg Harbor, New Jersey (Carriker, 1961), those researchers found that major peak of larval abundance occurred 8 - 10 days after full or new moon, concomitant with neap tides. The abundance of the larvae showed minor peaks in the intervening periods.

Wind induced circulation is another influential factor on the dispersion of bivalve larvae, besides tidal circulation. Prevailing winds blowing from one direction may induce currents (Perkins, 1974), which produce a net - horizontal transport of water on the surface (Ippen, 1966; Perkins, 1974; Tett, 1987). In St. Mary's River estuary, Maryland, according to Manning and Whaley (1954),

the pattern of longitudinal circulation is strongly influenced by prevailing southerly winds and provides a means of slow up-estuary transport and insures retention of the larvae in the upper estuary. The St. Mary's River is characterized by having low riverine discharge and high spatfalls on the upriver beds. Additionally, wind driven circulation has the potential for dispersing larvae from the spawning beds. In the Choptank River system, Maryland, prolonged down - estuary winds dilute out the retained larvae of two tributaries constituting major spawning areas, and carry the larvae down-estuary (Seliger et al., 1982).

In respect to temporal distribution, Landers (1954), Carriker (1961), and Rice and Goncalo (1995) established the fact that the peak of bivalve larval abundances occurred as water temperature reached about 20 °C, as summer progresses. During three consecutive years (1950, 1951, and 1952) of his study in Greenwich Bay and Wickford, Rhode Island, Landers found no consistent distributional pattern of quahog larvae from summer to summer. This may have been caused by variations in water temperature that stimulates spawning. Water temperature in 1950 was consistently lower than in either 1951 or 1952. This condition may explain the late beginning of spawning and occurrence of quahog larvae in that year. In spite of these variations, the population of quahog larvae at both sites reached the peak abundances in June as water temperature increased approximately to 19.0 °C. Carriker (1961) seemed to agree with Landers' opinion that variations of water temperature, in the course of his four successive year study, accounted for the variations of quahog larval abundance in Little Egg Harbor, New Jersey. However, in his study of oyster larvae near Oösterschelde, Holland, Korringa (1947) attempted to show but failed to prove that the peak of larval abundance depends upon water temperature.

Additional knowledge of distribution and abundance of larvae might explain their ability to maintain adult bivalve populations within estuaries (Haven and Fritz, 1987). In this study I tested hypotheses designed to enhance knowledge of Narragansett Bay quahog populations.

Hypotheses

The hypotheses evaluated for early stage and late stage quahog larvae in this study are :

1. Daily water temperatures affect the temporal distribution of the larvae ;
2. Spring and neap tides affect the abundances of quahog larvae;
3. The abundance of quahog larvae vary spatially due to variations of adult quahog density;
4. Larval abundance varies between two sampling depths.

MATERIALS AND METHODS

Study Area

Narragansett Bay is a major estuary in Rhode Island; and considered as the largest one in southern New England (Figure 1). Its location is surrounded by four coastal areas : Long Island Sound, Block Island Sound, Rhode Island Sound, and Buzzard's Bay (Spaulding, 1987). This system "...is composed of three north-south interconnected passages : a) West Passage, b) East Passage and the Providence River, and c) the Sakonnet River..." (Hicks, 1959).

Narragansett Bay is 40 km in length (Gordon, 1982); the surface area, shoreline length, and mean water volume are about 328 km², 412.5 km, and 2,724 km³, respectively (Chinman and Nixon, 1985; Spaulding, 1987). Mean water depth is 8.3 m, however, the depth of East Passage tends to be greater by a factor of two to West Passage and Sakonnet River (Spaulding, 1987). There are three major rivers discharging into Narragansett Bay : a) Blackstone River, b) Pawtuxet River, and c) Taunton River and Seekonk River (Spaulding, 1987). The first two rivers discharge into the Providence River, while the last one empties into Mount Hope Bay (Spaulding, 1987). The mean discharge of the Blackstone, Pawtuxet, and Taunton are 20, 11, and 19 m³/s, respectively (Spaulding, 1987). The mean residence time of Narragansett Bay water is about 26 days (Pilson, 1985).

Circulation in Narragansett Bay is due mainly to strong tidal currents (Levine and Kenyon, 1975), with gravitational induced by horizontal pressure gradients and wind-driven currents superimposed (Hess, 1976). This estuary is classified as a partially-mixed estuary, which means that the halocline dissipates and salinity increases gradually from surface to bottom (Pilson, 1985). Salinity

decreased from the entrance to the head of the Bay; 31 ppt at the entrance, while at the head values in the range of 10-20 ppt (Hicks, 1959). A salinity difference of only 2 ppt from surface to bottom is common (Gordon and Spaulding, 1987). Temperature increased from the entrance to the head with the difference of about 3 °C from surface to bottom (Hicks, 1959).

Field sampling

This study was conducted at five sampling stations in Narragansett Bay (Figure 1). A description of the sampling location is as follows. The most northerly station, Conimicut Pt. ($41^{\circ} 43'$), was located approximately 500 m southeast of Conimicut Point. The second station is Rocky Pt. ($41^{\circ} 41.5'$) which was about 500 m in front of Rocky Point amusement park shore. Warwick Pt. ($41^{\circ} 40.5'$), the third station, was located approximately 1 km northeast of Warwick neck. Those stations are situated on the Upper Bay. The last two stations, Mt. View ($41^{\circ} 38'$) which was about 4 km south of the mouth of Greenwich Bay and Wickford ($41^{\circ} 34.8'$) which was about 3 km off Wickford Cove are located on the Upper West Passage. Those five sampling stations were selected with regard to a declining trend of adult quahog densities from upper to lower estuary (Pratt, 1988; Kremer, 1975). The sampling was carried out every two days per week during summer of 1995, from May 26 to August 30. Due to strong winds and wave on particular days, samplings were postponed for safety reasons.

Water samples were collected haphazardly with respect to tides, using a 12 volt battery electric bilge pump, at two depths, 0.3 m and 1.6 m, at each station, similar to the method of Landers (1954). Prior to sampling collections, the electric bilge pump flow rate was calibrated by counting the amount of time required for pumping a 100 liter of water sample. The water samples were then filtered with a

60 µm mesh plankton net. Retained plankton samples were fixed with 95 % ethanol. Both surface water temperature and salinity in each station were measured. Tides and tidal current charts (Spaulding et al., 1990) were used to provide an information on the height of tides and velocity of tidal currents at the sampling stations.

Laboratory Analyses

In the laboratory, retained plankton samples were transferred to 30 ml mixture of 25 % ethanol and 75 % seawater. Three replicates of 1.0 ml subsamples of the preserved plankton were pipeted into a Sedgewick Rafter counting chamber. These subsamples were observed and counted using a stereoscopic microscope. To assist the progress of the identification, larval dimensions such as total, height, and hinge length were measured by using an image analysis (Optimas 4.0 software). Shape and dimension of the larvae were compared with photomicrographs provided by Loosanoff et al. (1966) and Chanley and Andrews (1971). The quahog larvae were categorized into two developmental stages. The early stage or straight-hinge larvae were characterized by a length of the hinge at least half of the total length. The late stage or umbonate stage was characterized as having hinge less than half of the total length and umbo begins to form.

Enumeration of Larvae

Numbers of larvae per 100 liter water sample (N) were calculated :

$$N = n \times v \quad (1)$$

where n = average number of larvae per 1.0 ml subsample, and v = volume of mixture 25 % ethanol and 75 % seawater = 30 ml.

Estimation of Mortality Rate

Rate of mortality of the quahog larvae was estimated by first calculating the rate of survival using the following method (Royce, 1984) :

$$S = N_{t+1} / N_t \quad (2)$$

where S = survival rate, N_{t+1} = number of larvae at late stage, N_t = number of larvae at early stage. A cohort, herein, was defined as a group of larvae at an early stage developing into the late stage within two weeks. Thus, rate of mortality (M) was obtained from :

$$M = 1 - S \quad (3)$$

Statistical Analyses

To investigate the relationship between larval abundance (Y) and water temperature (X), a linear correlation analysis was used.

$$r = \frac{S_{xy}}{\sqrt{S_{xx}} \sqrt{S_{yy}}} \quad (4)$$

where

$$S_{xy} = \Sigma(x - \bar{x})(y - \bar{y}) ; S_{xx} = \Sigma(x - \bar{x})^2 ; S_{yy} = \Sigma(y - \bar{y})^2$$

In addition, a qualitative evaluation of the water temperature required to trigger quahog spawning in Narragansett Bay was made by comparing the temporal variation in temperature with the temporal variation in larval abundances.

A Wilcoxon Rank-Sum Test was used to examine : (1) the abundances of quahog larvae during neap tides vs spring tides; (2) the abundances of quahog larvae at 0.3 m vs 1.6 m depths. The procedure is as follow :

1. Assign H_0 : the populations are identical. Populations, herein, were determined as larval abundances during neap tides vs during spring tides and larval abundances at 0.3 m vs 1.6 m depths.
2. Rank the combined value of $n = n_A + n_B$ observations in the increasing order of magnitude. Where n = total number of observation, n_A = number of observation in which larval abundances in condition A (i.e., during neap tides, or at 0.3 m depths), n_B = number of observation in which larval abundances in condition B (i.e., during spring tides, or at 1.6 m depth).
3. Find the rank sum W_A of the first sample of population having smaller sum of the ranks.
4. Assign H_1 : the populations are different ; then the rejection region (R) at both tails of W_A (lower and upper tails) having equal probabilities.
5. Assign R : $P = P [W_A \leq x^*] = P [W_A \geq x]$.

Since the sample sizes were larger than 8, the null distribution of the rank-sum statistic is approximately normal and the Wilcoxon test can therefore be performed using the normal table (Johnson and Bhattacharya, 1992). Under H_0 , the distribution of W_A has

$$\text{mean} = 1/2 \{n_A (n_A + n_B + 1)\}, \text{ and variance} = \{n_A n_B (n_A + n_B + 1)\} / 12$$

$$Z = \left(W_A - \text{mean} \right) / \sqrt{\text{variance}} \quad (5)$$

Therefore, the rejection region to be :

$$R : | Z | \geq Z_{\alpha/2}$$

To determine if the abundance of quahog larvae varies among stations due to variations of adult quahog, the Kruskal-Wallis method was used because there are more than two stations as independent variables. This test is based on the ranks of the observation.

1. $H_0 : \mu_1 = \dots = \mu_5$. Where μ_j is the mean of larval abundances in the given station.
2. $H_1 : \mu_1 \neq \dots \neq \mu_5$
3. All observations are ranked from 1 to n. Let R_i be the mean of the ranks for the i th factor level and $R_{..}$ the overall mean rank.
4. Test statistic :

$$X_{KW}^2 = \left(\frac{12}{n(n+1)} \sum_{i=1}^r n_i R_i^2 \right) - 3(n+1) \quad (6)$$

5. $R : X_{KW}^2 > \chi^2(1 - \alpha; r-1)$

Multiple regression analysis was used for the purpose of constructing a model for prediction in this study. The dependent variable to be assigned in this study is the abundance of quahog larvae (Y), and the independent variables are depths (x_1), moon phase (x_2) in respect to spring and neap tides, water temperature (x_3), and stations (x_4). A full model of multiple regression is :

$$Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \beta_4 x_{i4} + \epsilon_i \quad (7)$$

where $i = 1, 2, \dots, n$

Stepwise regression analysis was also performed, using SAS software, to examine a better linear regression model.

RESULTS

Physical Environment

Data of surface water temperature and salinity are presented in Table 1. Water temperature measured during the summer of 1995 ranged from 16.0 to 26.5 °C. During the early summer, the average water temperature was 19.7 °C. Temperature reached the highest point on July 28 (209th Julian day), 26.1 °C in average. The temperature, then, gradually decreased.

Salinities were higher at Upper West Passage stations than those at stations of Upper Bay. The range was between 28 and 31 ppt at Upper West Passage stations; while at Upper Bay stations, salinity was between 26 and 29 ppt.

Distribution of Larvae

A total of 150 bivalve larval collections were taken from two depths (0.3 and 1.6 m) at five sampling stations in Narragansett Bay during summer 1995, from May 26 (146th Julian day) to August 30 (242nd Julian day) (Table 2 and 3). The average percentage of quahog larvae relative to other bivalve larvae was 40 %. Concentration ranges of total, early stage, and late stage quahog larvae were 0 - 19,740 larvae, 0 - 19,680, and 0 - 420 larvae per 100 l, respectively. The quahog larvae in Upper Bay stations outnumbered those in stations of Upper West Passage. The early stage larvae were concentrated more in Rocky Pt., while the late ones were in Conimicut Pt., both stations located in Upper Bay. Other bivalve larvae ranged 0 - 15,840 total larvae, 0 - 15,390 early stage

larvae, and 0 - 1,470 late stage larvae per 100 l. Those larvae tended to concentrate also in Upper Bay stations.

Temporal distributions of *Mercenaria mercenaria* and other bivalve larvae, associated with daily water temperatures, are illustrated in Figures 2 to 11. The pattern of larval distributions in Wickford differed from those in other stations. The quahog larvae in Wickford were more concentrated in the early sampling days, as water temperatures were less warm. On the other hand, the larvae in other stations tended to invade water column as water temperatures got warmer.

On the first sampling day (May 26), temperature was about 16 °C, early stage quahog larvae were only 4.9 - 45.8 percent of the total early stage bivalve larvae. The densities were higher at Upper Bay stations, Conimicut Pt. (1,965 larvae per 100 l), Rocky Pt. (135 larvae per 100 l), and Warwick Pt. (555 larvae per 100 l), than those at Upper West Passage stations, Mt. View (150 larvae per 100 l) and Wickford (60 larvae per 100 l). The late stage of quahog larvae comprised only 0 - 15.9 percent of the total late stage bivalve larvae. Numbers of quahog larvae at the late stage in Conimicut Pt., Warwick Pt., Mt. View, and Wickford were 45, 20, 15, and 5 larvae per 100 l, respectively. No larva was present in the plankton samples taken from Rocky Pt.

Peak abundances of early stage larvae, age 1-3 days, occurred on June 20 (171st Julian day) at Conimicut Pt. (11,365 larvae per 100 l), Rocky Pt. (12,810 larvae per 100 l), Warwick Pt. (6,155 larvae per 100 l), and Mt. View (3,595 larvae per 100 l). The peak abundances coincided with increase water temperatures to above 20 °C. Quahog larvae predominated the population of bivalve larvae (as high as 72.5 percent). Early stage larval densities declined following the peak of June 20; average abundances were 639, 675, 287, and 291 larvae per 100 l at Conimicut Pt., Rocky Pt., Warwick Pt., and Mt. View,

respectively. The larvae at Wickford, however, showed different pattern. The maximum abundance (3,775 larvae per 100 l) occurred 11 days earlier (June 9) than that at other stations, where water temperature was only 19.5 °C when the peak occurred. Abundances, afterward, were less than 325 larvae per 100 l.

Maximum numbers of late stage veligers were observed on July 7 (188th Julian day) with abundances 165, 60, 230, and 65 larvae per 100 l in respect to Conimicut Pt., Rocky Pt., Warwick Pt., and Mt. View. At Wickford, the peak of 40 larvae per 100 l on July 7 was not considered to be the maximum concentration since it was only at the factor of 1.5 lower than the peak on June 9 - 160th Julian day - (65 larvae per 100 l).

In respect to lunar phase, the peak abundances of quahog larvae generally occurred 6 to 12 days after new moon or full moon, and coincided with neap tides (Figure 12). During the intervening periods, the quahog larvae showed lower abundances. The evidence of major peak abundance of June 20 fell within a period of neap tide.

Mortality

As it is assumed that larval duration is about 2 to 3 weeks, the rate of survival of quahog larvae was estimated by calculating the ratio of late and early stage larvae with a time lag of 11 - 17 days. The rate of mortality was obtained by subtracting the survival rate from 1. Table 4 shows the rate of mortality of quahog larvae in Narragansett Bay which ranged from 80 to 99 %. Detailed calculation for mortality rate is presented on Appendix A.

Statistical Analyses

This study evaluated four hypotheses. Linear correlation analysis was performed to detect an association between water temperature and abundances of quahog larvae. The correlation coefficients (r) were relatively small, ranging between - 0.28 and - 0.04 (Figure 13 - 17). These small numbers indicated that the relationship between water temperature and larval abundance is weak or there is almost no distinct relationship between these two variables, thus, the linear regression model does not seem to give a good fit to the data (Johnson and Bhattacharya, 1992).

A non parametric procedure utilized for comparing larval abundances in neap and spring tides demonstrated a significant difference (Table 5). This study, therefore, supports previous studies (Korringa, 1947; Carriker, 1961) which reported that the abundances of bivalve larvae were different during neap and spring tides. Another test proved that there was a significant difference among the abundances of quahog larvae in five sampling stations (Table 6). There is enough evidence to claim that the larval abundances were different among five sampling stations. However, this procedure failed to reject the null-hypothesis for testing the effects of depths on the larval abundances (Table 7). The present study failed to support the result of the Rice and Goncalo study (1994) that early stage larvae were found in higher number at upper water column (0.3 meter).

Coefficient of determination (r^2) in multiple regression models determines how much variation of dependent variable can be accounted for by the model. Table 8 presents the result of multiple regression analysis between larval abundance and independent variables, i.e., water temperature, moon phase, stations, and depths. This full model, which included all variables, provided a very

low r^2 (0.20). Thus, only 20 % of the variation in the abundances of quahog larvae in Narragansett Bay can be explained by all of those independent variables.

A partial analysis of multiple regression (stepwise method) showed that the simpler model, which included only moon phase, had small r^2 of 0.09 (Table 9). By adding another independent variable (stations), r^2 increased to 0.18 (Table 10). It appears that two other variables were not added into the model, because those, probably, gave less contribution to the increase of r^2 .

Table 1. Temperature (degree C) and salinity (ppt) at five sampling stations in Narragansett Bay during summer 1995. T, temperature; S, salinity; N/A, data not available; Numbers in parentheses denote Julian day.

Date	Conimicut Pt.		Rocky Pt.		Warwick Pt.		Mt. View		Wickford	
	T	S	T	S	T	S	T	S	T	S
26-May (146)	16.50 12:00	26	16.50 12:40	27	16.50 13:28	27	16.50 14:20	29	16.00 16:20	31
31-May (151)	17.00 11:00	27	17.50 11:52	27	17.50 12:40	28	18.00 13:25	28	N/A	N/A
9-Jun (160)	18.00 9:05	27	18.50 10:06	28	19.00 10:36	28	19.50 11:21	29	19.50 12:01	30
14-Jun (165)	17.00 10:32	26	17.00 11:21	26	16.50 12:08	28	17.00 13:05	30	17.00 3:10	31
20-Jun (171)	23.00 10:45	27	22.00 11:45	27	23.00 12:20	27	22.00 13:15	29	22.00 14:52	31
28-Jun (179)	20.00 10:30	27	20.00 11:10	28	20.50 11:55	28	21.50 12:30	29	22.00 13:30	30
7-Jul (188)	22.50 10:30	28	22.50 11:20	28	23.00 12:08	29	22.00 12:50	30	21.50 14:45	31
13-Jul (194)	21.50 10:30	27	22.00 11:15	27	22.00 11:55	28	22.50 12:30	29	22.00 14:35	29

Table 1. Continued

Date	Conimicut Pt.		Rocky Pt.		Warwick Pt.		Mt. View		Wickford	
	T	S	T	S	T	S	T	S	T	S
19-Jul (200)	22.50 11:20	28	22.50 12:00	28	23.00 12:50	29	23.50 13:35	30	22.50 14:25	30
28-Jul (209)	26.50 10:45	27	26.50 11:20	27	26.50 11:50	27	26.00 12:30	29	25.00 14:30	31
4-Aug (216)	25.00 9:40	26	25.00 10:15	27	25.00 10:40	28	25.00 11:20	29	25.00 12:05	29
9-Aug (221)	22.50 11:00	27	22.50 11:30	28	22.50 12:00	29	23.50 12:35	30	23.50 13:30	31
14-Aug (226)	24.00 10:37	27	24.00 11:10	28	24.00 11:35	28	23.50 12:10	30	24.00 12:55	30
23-Aug (235)	22.00 10:35	28	22.00 11:15	28	22.50 11:45	28	23.00 12:30	29	23.00 13:00	31
30-Aug (242)	21.00 10:55	27	21.00 11:30	27	21.50 12:00	28	22.00 12:35	29	21.50 13:20	31

Table 2. Densities of quahog larvae (per 100 l) at two sampling depths in five stations of Narragansett Bay during summer 1995. T, total larvae; E, early stage larvae (see text); L, late stage larvae (see text); N/A, data not available; Numbers in parentheses denote Julian day.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
26-May (146)	0.30	1830	1810	20	20	20	0	340	330	10	60	60	0	40	40	0
	1.60	2190	2120	70	250	250	0	810	780	30	270	240	30	90	80	10
			12:00			12:40			13:28			14:20			16:20	
31-May (151)	0.30	60	60	0	40	40	0	70	70	0	130	130	0	N/A	N/A	N/A
	1.60	760	720	40	60	60	0	190	150	40	210	200	10	N/A	N/A	N/A
			11:00			11:52			12:40			13:25				
9-Jun (160)	0.30	2870	2850	20	4410	4410	0	1340	1310	30	340	340	0	690	690	0
	1.60	990	980	10	3580	3580	0	1950	1920	30	1780	1710	70	6990	6860	130
			9:05			10:06			10:36			11:21			12:01	
14-Jun (165)	0.30	100	100	0	60	40	20	90	90	0	60	40	20	240	200	40
	1.60	210	190	20	200	200	0	120	120	0	90	80	10	90	90	0
			10:32			11:21			12:08			13:05			3:10	
20-Jun (171)	0.30	7760	7760	0	5950	5940	10	6820	6820	0	5710	5700	10	80	80	0
	1.60	14970	14970	0	19740	19680	60	5500	5490	10	1500	1490	10	80	80	0
			10:45			11:45			12:20			13:15			14:52	
28-Jun (179)	0.30	230	230	0	290	290	0	550	540	10	340	340	0	210	210	0
	1.60	1060	970	90	850	840	10	1930	1870	60	710	680	30	220	220	0
			10:30			11:10			11:55			12:30			13:30	

Table 2. Continued.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
7-Jul (188)	0.30	20	20	0	1660	1580	80	450	410	40	990	920	70	680	620	60
	1.60	3270	2940	330	1800	1760	40	480	60	420	1350	1290	60	50	30	20
			10:30			11:20			12:08			12:50			14:45	
13-Jul (194)	0.30	30	20	10	160	150	10	40	30	10	80	70	10	90	90	0
	1.60	720	670	50	40	30	10	20	20	0	60	40	20	10	10	0
			10:30			11:15			11:55			12:30			14:35	
19-Jul (200)	0.30	300	180	120	1750	1700	50	40	40	0	240	230	10	70	70	0
	1.60	1410	1280	130	50	30	20	584	560	24	310	270	40	110	100	10
			11:20			12:00			12:50			13:35			14:25	
28-Jul (209)	0.30	920	920	0	1060	1020	40	60	60	0	10	10	0	170	170	0
	1.60	20	0	20	70	60	10	400	400	0	540	540	0	0	0	0
			10:45			11:20			11:50			12:30			14:30	
4-Aug (216)	0.30	20	20	0	4800	4800	0	1070	1070	0	60	50	10	80	80	0
	1.60	4260	4240	20	60	50	10	30	30	0	980	980	0	440	420	20
			9:40			10:15			10:40			11:20			12:05	
9-Aug (221)	0.30	0	0	0	0	0	0	90	90	0	40	40	0	40	40	0
	1.60	100	100	0	100	90	10	30	30	0	60	30	30	20	20	0
			11:00			11:30			12:00			12:35			13:30	

Table 2. Continued.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
14-Aug (226)	0.30	40	40	0	30	20	10	50	50	0	20	20	0	20	20	0
	1.60	80	60	20	80	60	20	0	0	0	40	30	10	50	50	0
			10:37			11:10			11:35			12:10			12:55	
23-Aug (235)	0.30	0	0	0	0	0	0	90	90	0	30	30	0	0	0	0
	1.60	960	930	30	770	750	20	70	40	30	30	20	10	30	30	0
			10:35			11:15			11:45			12:30			13:00	
30-Aug (242)	0.30	10	10	0	120	120	0	10	10	0	210	210	0	0	0	0
	1.60	150	150	0	150	140	10	330	330	0	20	20	0	120	120	0
			10:55			11:30			12:00			12:35			13:20	
Average		1511	1478	33	1605	1590	15	785	760	25	542	527	15	383	372	10

Table 3. Densities of other bivalve larvae (per 100 l) at two sampling depths in five stations of Narragansett Bay during summer 1995. T, total larvae; E, early stage larvae (see text); L, late stage larvae (see text); N/A, data not available; Numbers in parentheses denote Julian day.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
26-May (146)	0.30	9450	9420	30	30	30	0	3180	3120	60	1710	1620	90	1160	1120	40
	1.60	15840	15390	450	300	290	10	5440	5140	300	1760	1650	110	1240	1200	40
			12:00			12:40			13:28			14:20			16:20	
31-May (151)	0.30	80	60	20	100	100	0	110	110	0	230	190	40	N/A	N/A	N/A
	1.60	3730	3540	190	200	170	30	410	320	90	660	600	60	N/A	N/A	N/A
			11:00			11:52			12:40			13:25				
9-Jun (160)	0.30	1920	1890	30	1950	1950	0	750	720	30	420	390	30	240	240	0
	1.60	660	660	0	1890	1830	60	990	990	0	1440	1350	90	2310	2250	60
			9:05			10:06			10:36			11:21			12:01	
14-Jun (165)	0.30	330	240	90	480	390	90	420	420	0	240	210	30	1620	1560	60
	1.60	810	600	210	990	870	120	600	510	90	540	450	90	690	570	120
			10:32			11:21			12:08			13:05			3:10	
20-Jun (171)	0.30	1810	1780	30	2400	2400	0	4640	4590	50	5630	5520	110	2190	2150	40
	1.60	7170	7170	0	7380	7340	40	2820	2790	30	1390	1390	0	1820	1770	50
			10:45			11:45			12:20			13:15			14:52	
28-Jun (179)	0.30	390	330	60	200	200	0	350	350	0	140	110	30	340	340	0
	1.60	2250	1770	480	580	480	100	1610	1370	240	610	430	180	390	390	0
			10:30			11:10			11:55			12:30			13:30	

Table 3. Continued.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
7-Jul (188)	0.30	1020	930	90	3430	2810	620	670	520	150	2770	2020	750	3600	3040	560
	1.60	5930	4510	1420	4960	4560	400	3980	3600	380	3080	2520	560	650	580	70
			10:30			11:20			12:08			12:50			14:45	
13-Jul (194)	0.30	330	310	20	520	430	90	400	370	30	510	460	50	160	150	10
	1.60	190	180	10	260	220	40	150	120	30	160	130	30	400	340	60
			10:30			11:15			11:55			12:30			14:35	
19-Jul (200)	0.30	3620	3400	220	3780	3210	570	250	250	0	1200	920	280	1820	1730	90
	1.60	2500	2160	340	710	570	140	1630	1580	50	1580	1500	80	3880	3770	110
			11:20			12:00			12:50			13:35			14:25	
28-Jul (209)	0.30	1360	1330	30	2490	2140	350	180	150	30	350	300	50	660	610	50
	1.60	810	780	30	630	570	60	740	660	80	860	780	80	70	60	10
			10:45			11:20			11:50			12:30			14:30	
4-Aug (216)	0.30	1430	1160	270	3450	3240	210	1840	1770	70	1920	1490	430	420	360	60
	1.60	770	690	80	760	610	150	470	320	150	1390	1300	90	840	800	40
			9:40			10:15			10:40			11:20			12:05	
9-Aug (221)	0.30	110	60	50	30	20	10	150	130	20	0	0	0	180	130	50
	1.60	150	120	30	130	90	40	90	60	30	260	220	40	70	50	20
			11:00			11:30			12:00			12:35			13:30	

Table 3. Continued.

Date	Depth (m)	Conimicut Pt.			Rocky Pt.			Warwick Pt.			Mt. View			Wickford		
		T	E	L	T	E	L	T	E	L	T	E	L	T	E	L
14-Aug (226)	0.30	1780	1540	240	3470	3150	320	1180	1070	110	20	20	0	260	240	20
	1.60	70	40	30	200	150	50	150	130	20	1780	1710	70	1070	1050	20
			10:37			11:10			11:35			12:10			12:55	
23-Aug (235)	0.30	150	120	30	70	50	20	620	600	20	3540	2070	1470	20	20	0
	1.60	3180	3000	180	3030	2280	750	0	0	0	30	30	0	1020	870	150
			10:35			11:15			11:45			12:30			13:00	
30-Aug (242)	0.30	40	30	10	240	150	90	0	0	0	540	540	0	30	30	0
	1.60	1080	960	120	450	410	40	1080	900	180	20	20	0	630	630	0
			10:55			11:30			12:00			12:35			13:20	
Average		2299	2139	160	1504	1357	147	1163	1089	75	1152	998	161	992.1	930.4	62

Table 4. Rate of mortality of quahog larvae in Narragansett Bay during summer 1995. Cohort is defined as a group of larvae at an early stage developing into the late stage within 11 - 17 days.

cohort	Mortality
1	94.90%
2	93.80%
3	99.60%
4	82.60%
5	98.35%
6	98.06%
7	95.80%
8	93.81%
9	98.65%
10	98.74%
11	99.49%
12	79.55%
13	97.14%

Table 5. Non-parametric procedure to determine whether there is a difference between abundances of quahog larvae during neap (N.T) and spring (S.T) tides in Narragansett Bay in the summer of 1995.

N.T	RANK	S.T	RANK
0	4.5	0	4.5
0	4.5	0	4.5
10	10.5	0	4.5
10	10.5	0	4.5
20	17	0	4.5
20	17	0	4.5
20	17	10	10.5
20	17	10	10.5
20	17	20	17
20	17	20	17
30	25	20	17
30	25	30	25
40	33	30	25
40	33	30	25
40	33	30	25
40	33	30	25
50	39.5	40	33
50	39.5	40	33
50	39.5	40	33
50	39.5	40	33
60	46.5	40	33
60	46.5	60	46.5
60	46.5	60	46.5
70	53.5	60	46.5
80	58.5	60	46.5
80	58.5	60	46.5
80	58.5	60	46.5
80	58.5	60	46.5
80	58.5	70	53.5
90	65	70	53.5
110	72	70	53.5
120	74	80	58.5
120	74	90	65
150	77.5	90	65
150	77.5	90	65
210	84.5	90	65
240	89.5	90	65
250	91	90	65
270	92	100	70

Table 5. Continued

N.T	RANK	S.T	RANK
300	94	100	70
310	95	100	70
330	96	120	74
340	98	130	76
340	98	160	79
440	101	170	80
450	102	190	81
480	103	200	82
584	106	210	84.5
680	107	210	84.5
810	112	210	84.5
980	116	220	87
990	118	230	88
990	118	240	89.5
1070	121	290	93
1340	122	340	98
1350	123	400	100
1410	124	540	104
1660	125	550	105
1750	126	710	108
1780	127	720	109
1800	128	760	110
1830	129	770	111
1950	131	850	113
2190	132	920	114
2870	133	960	115
3270	134	1060	120
3580	135	1060	120
4260	136	1930	130
4410	137		
4800	138		

$$W_A = 4172.5$$

Mean rank = 4726 ; Standard deviation = 234.8

$$Z = (W_A - \text{Mean rank}) / \text{Standard deviation} = - 2.36 ; Z_{\alpha/2} = - 1.96$$

$$R : |Z| \geq - 1.96$$

Since $Z = - 2.36$ falls in the rejection region, then H_0 is rejected

Table 6. Non-parametric test, using Kruskal-Wallis method, to determine whether there are differences of quahog larval abundances among five stations.

Date	Conimicut Pt.		Rocky Pt.		Warwick Pt.		Mt. View		Wickford	
	Larvae	Rank	Larvae	Rank	Larvae	Rank	Larvae	Rank	Larvae	Rank
26-May	2010	49	135	18	575	39	165	20	65	8
31-May	410	30	50	5	130	17	170	21	N/A	N/A
9-Jun	1930	48	3995	54	1645	46	1060	43	3840	53
14-Jun	155	19	130	17	105	15	75	10	165	20
20-Jun	11365	56	12845	57	6160	55	3605	52	80	11
28-Jun	645	40	570	38	1240	45	525	35	215	22
7-Jul	1645	46	1730	47	465	31	1170	44	365	27
13-Jul	375	28	100	14	30	3	70	9	50	5
19-Jul	855	41	900	42	312	26	275	25	90	13
28-Jul	470	32	565	37	230	23	275	25	85	12
4-Aug	2140	50	2430	51	550	36	520	34	260	24
9-Aug	50	5	50	5	60	7	50	5	30	3
14-Aug	60	7	55	6	25	2	30	3	35	4
23-Aug	480	33	385	29	80	11	30	3	15	1
30-Aug	80	11	135	18	170	21	115	16	60	7

$$H_0 : \mu_1 = \mu_2 = \dots = \mu_r$$

$$H_1 : \mu_1 \neq \mu_2 \neq \dots \neq \mu_r$$

$$R : \chi^2_{KW} > \chi^2_{(0.90;4)}$$

Since $\chi^2_{KW} = 4330.04$ that is greater than $\chi^2_{(0.90;4)} = 7.78$, then H_0 is rejected.

Table 7. Non-parametric procedure to determine whether there is a difference between abundances of quahog larvae at two depths (0.3 and 1.6 m) in Narragansett Bay during summer 1995.

D-0.3	RANK	D-1.6	RANK
0	4.5	0	4.5
0	4.5	0	4.5
0	4.5	10	10.5
0	4.5	20	17
0	4.5	20	17
0	4.5	20	17
10	10.5	20	17
10	10.5	30	25
10	10.5	30	25
20	17	30	25
20	17	30	25
20	17	40	33
20	17	40	33
20	17	50	39.5
30	25	50	39.5
30	25	50	39.5
30	25	60	46.5
40	33	60	46.5
40	33	60	46.5
40	33	60	46.5
40	33	70	53.5
40	33	70	53.5
40	33	80	58.5
40	33	80	58.5
50	39.5	80	58.5
60	46.5	90	65
60	46.5	90	65
60	46.5	90	65
60	46.5	100	70
60	46.5	100	70
60	46.5	110	72
70	53.5	120	74
70	53.5	120	74
80	58.5	150	77.5
80	58.5	150	77.5
80	58.5	190	81
90	65	200	82
90	65	210	84.5
90	65	210	84.5

Table 7. Continued

D-0.3	RANK	D-1.6	RANK
90	65	220	87
100	70	250	91
120	74	270	92
130	76	310	95
160	79	330	96
170	80	400	100
210	84.5	440	101
210	84.5	480	103
230	88	540	104
240	89.5	584	106
240	89.5	710	108
290	93	720	109
300	94	760	110
340	98	770	111
340	98	810	112
340	98	850	113
450	102	960	115
550	105	980	116
680	107	990	117.5
920	114	1060	119.5
990	117.5	1350	123
1060	119.5	1410	124
1070	121	1780	127
1340	122	1800	128
1660	125	1930	130
1750	126	1950	131
1830	129	2190	132
2870	133	3270	134
4410	137	3580	135
4800	138	4260	136

$$W_A = 4617$$

Mean rank = 4795.5 ; Standard deviation = 234.8

$$Z = (W_A - \text{Mean rank}) / \text{Standard deviation} = -0.76 ; \quad Z_{\alpha/2} = -1.96$$

$$R : |Z| \geq Z_{\alpha/2}$$

Since $Z = -0.76$ does not fall in the rejection region, then H_0 is accepted.

Table 8. Result of multiple regression, x1, depth; x2, moon phase; x3, temperature; x4-x7, station.

Regression-Statistics

Multiple R	0.4444
R Square	0.1975
Adj. R Sq	0.1507
Std. Error	825.35
Observations	128

Analysis of Variance

	df	Sum of Squares	Mean Square	F	Significance F
Regression	7	2E+07	3E+06	4.219	0.0003
Residual	120	8.2E+07	681197		
Total	127	1E+08			

	Coefficients	Std. Error	t Statistic	P-value	Lower 95%	Upper 95%
Intercept	1106.9	624.792	1.7717	0.079	-130.1	2344
x1	127.72	145.902	0.8754	0.383	-161.16	416.6
x2	-545.01	146.259	-3.726	3E-04	-834.6	-255
x3	-35.008	26.7172	-1.31	0.192	-87.906	17.89
x4	597.06	234.107	2.5504	0.012	133.55	1061
x5	740.91	233.9	3.1676	0.002	277.81	1204
x6	276.64	233.86	1.1829	0.239	-186.38	739.7
x7	231.3	233.725	0.9896	0.324	-231.46	694.1

Table 9. Result of stepwise method, variable moon phase entered.

R square = 0.0897

	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	1	9E+06	9141420	12.42	6E-04
Error	126	9E+07	735887		
Total	127	1E+08			

Variable	Parameter Estimate	Standard Error	F	Prob>F
Intercept	772.73	110.75	6.9775	1E-10
Moon	-535.53	151.94	-3.5245	6E-04

Table 10. Result of stepwise method, variable stations entered. x1, moon phase; x2-x5, stations.

R square = 0.1809

	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	5	2E+07	3685609	5.389	2E-04
Residual	122	8E+07	683895		
Total	127	1E+08			

Variable	Parameter Estimate	Standard Error	F	Prob>F
Intercept	394.16	184.02	2.14193	0.034
x1	-546.7	146.54	-3.7304	3E-04
x2	615.19	234.16	2.62723	0.01
x3	753.65	234.16	3.21854	0.002
x4	288.04	234.16	1.23009	0.221
x5	235.96	234.16	1.00769	0.316

Figure 2. Distribution of bivalve larvae at early stage associated with temperature in Conimicut Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

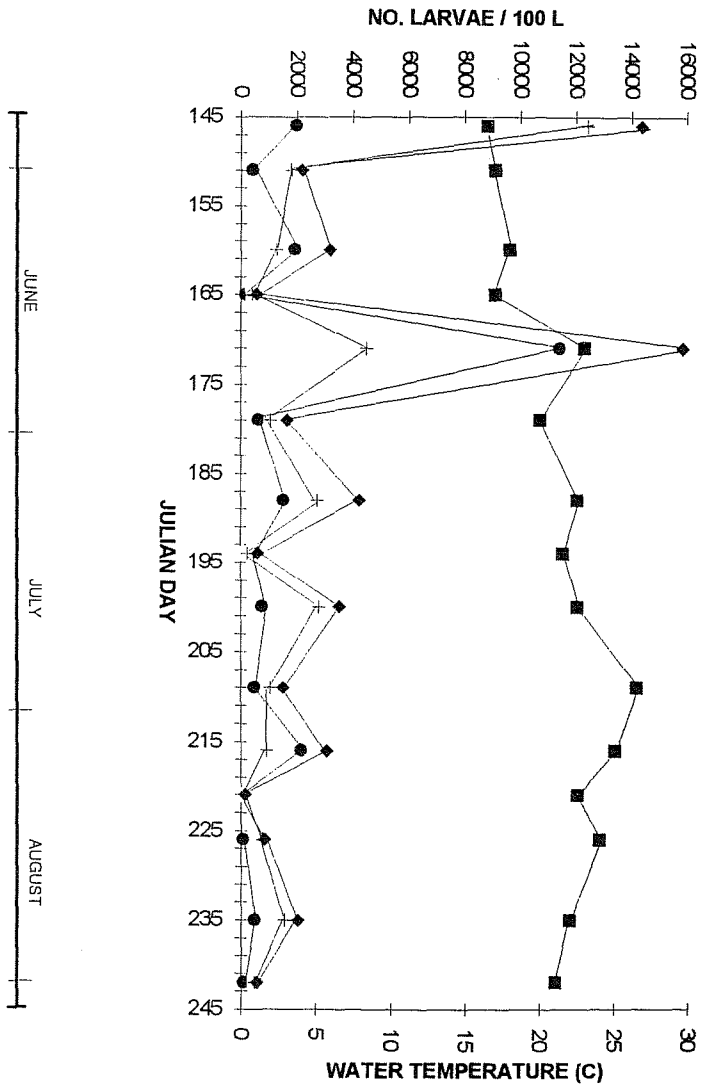


Figure 3. Distribution of bivalve larvae at late stage associated with temperature in Conimicut Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

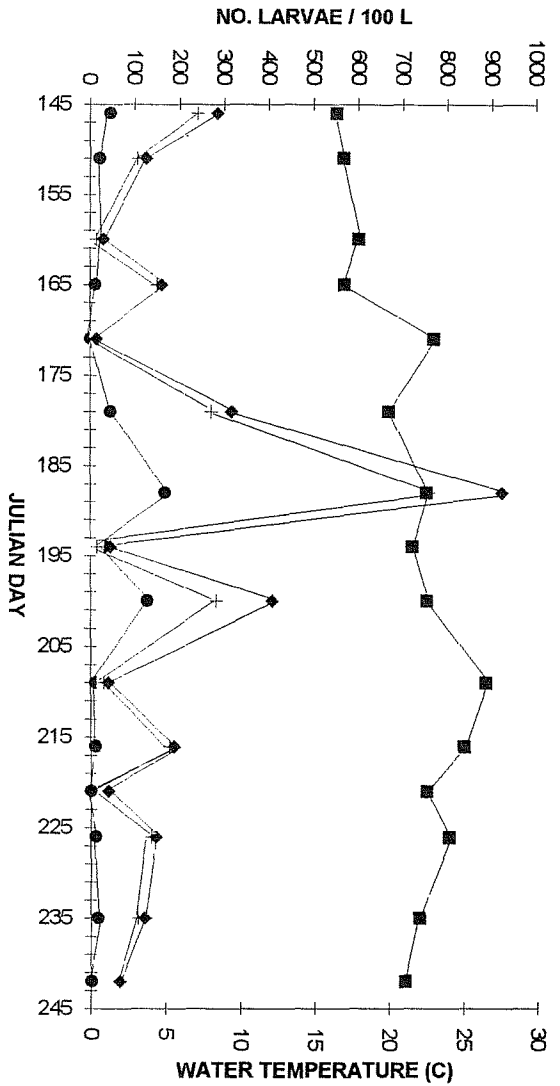


Figure 4. Distribution of bivalve larvae at early stage associated with temperature in Rocky Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

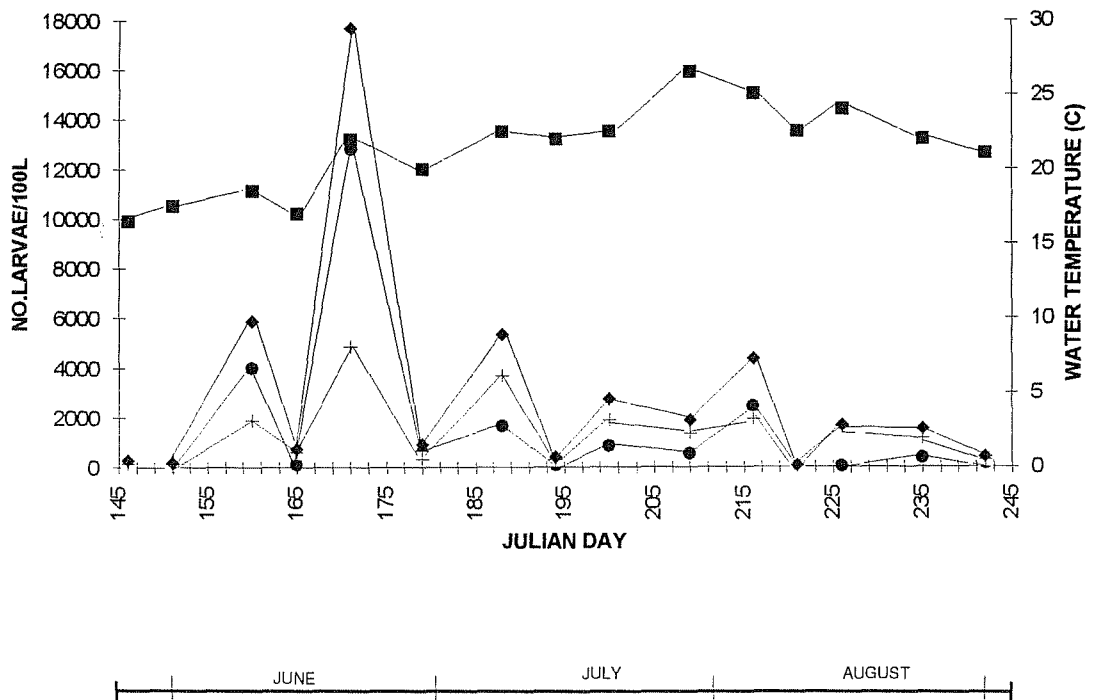


Figure 5. Distribution of bivalve larvae at late stage associated with temperature in Rocky Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

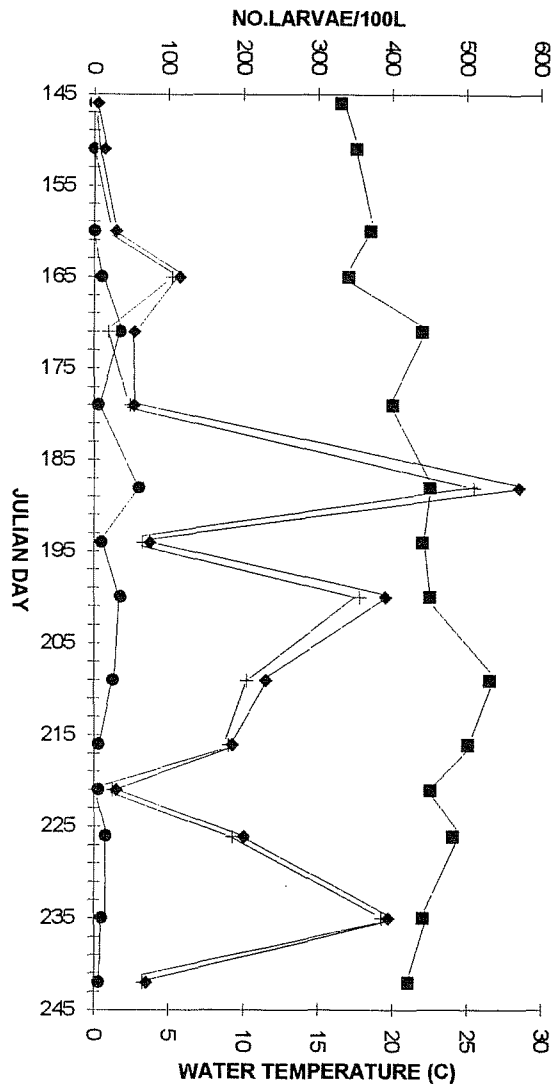


Figure 6. Distribution of bivalve larvae at early stage associated with temperature in Warwick Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

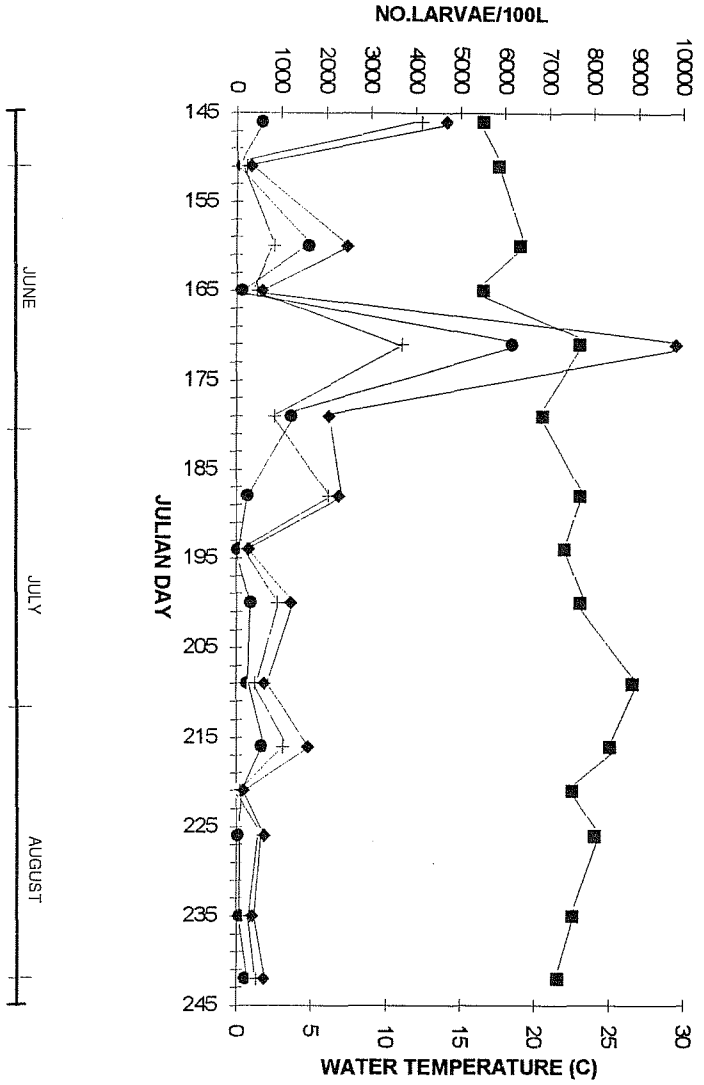


Figure 7. Distribution of bivalve larvae at late stage associated with temperature in Warwick Pt.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

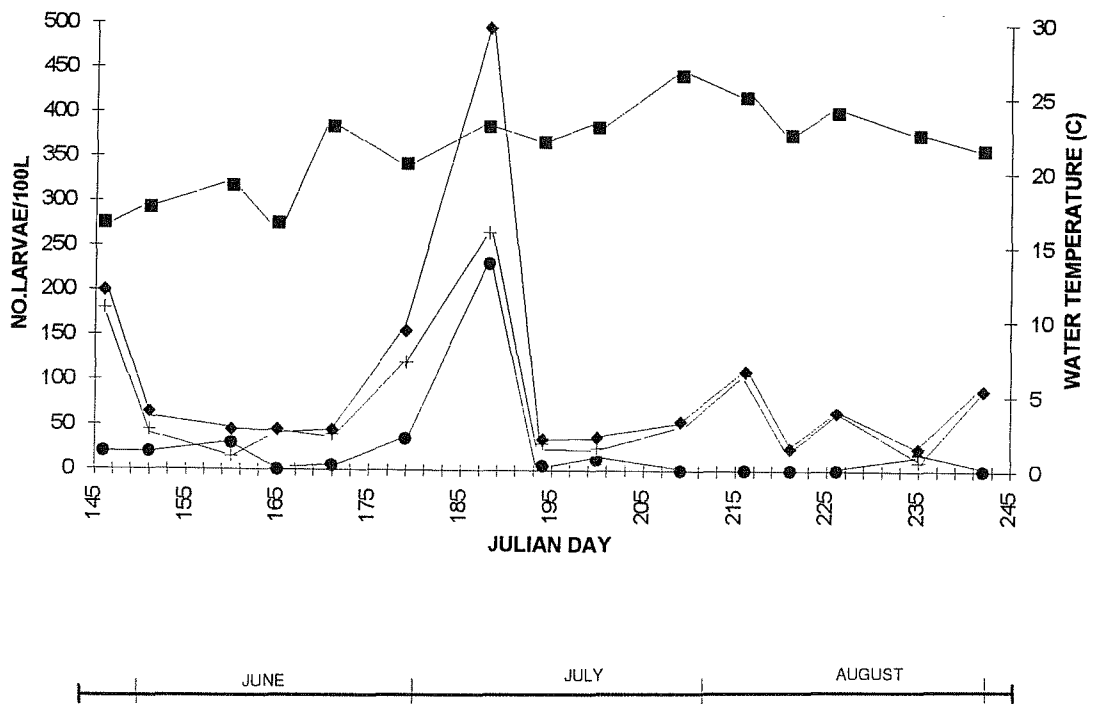


Figure 8. Distribution of bivalve larvae at early stage associated with temperature in Mt. View.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

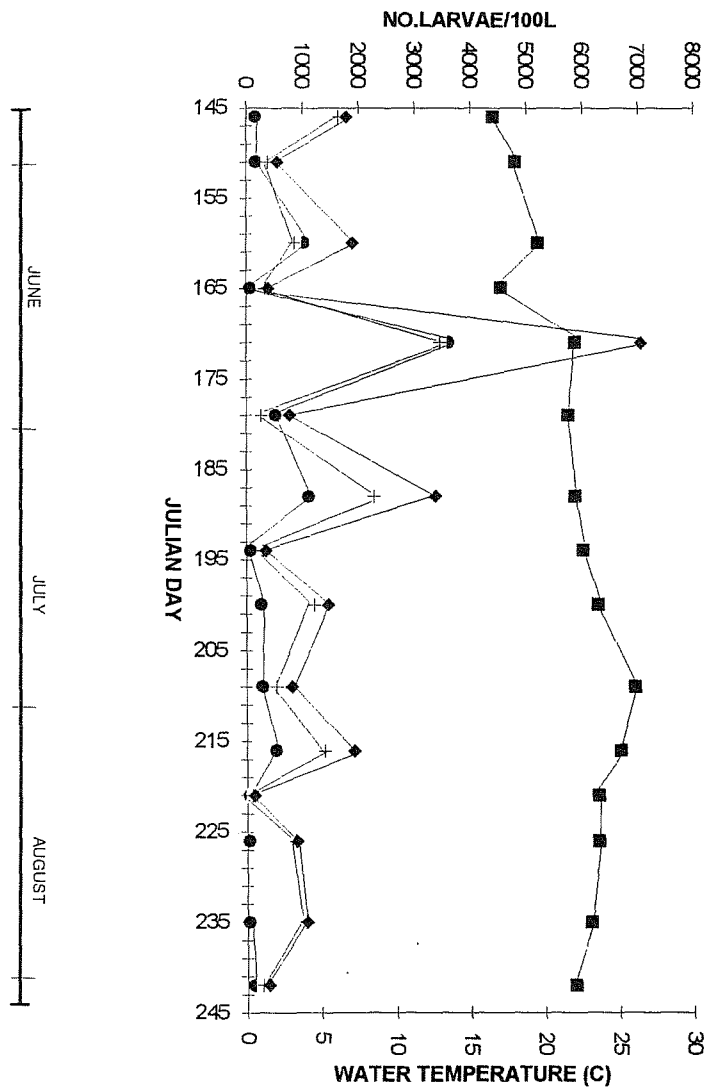


Figure 9. Distribution of bivalve larvae at late stage associated with temperature in Mt. View.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

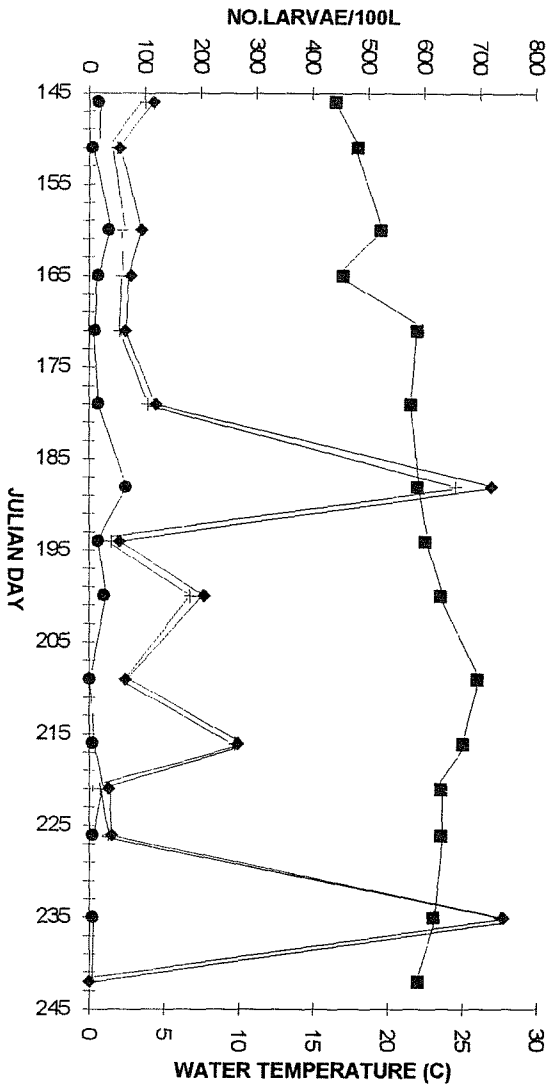


Figure 10. Distribution of bivalve larvae at early stage associated with temperature in Wickford.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

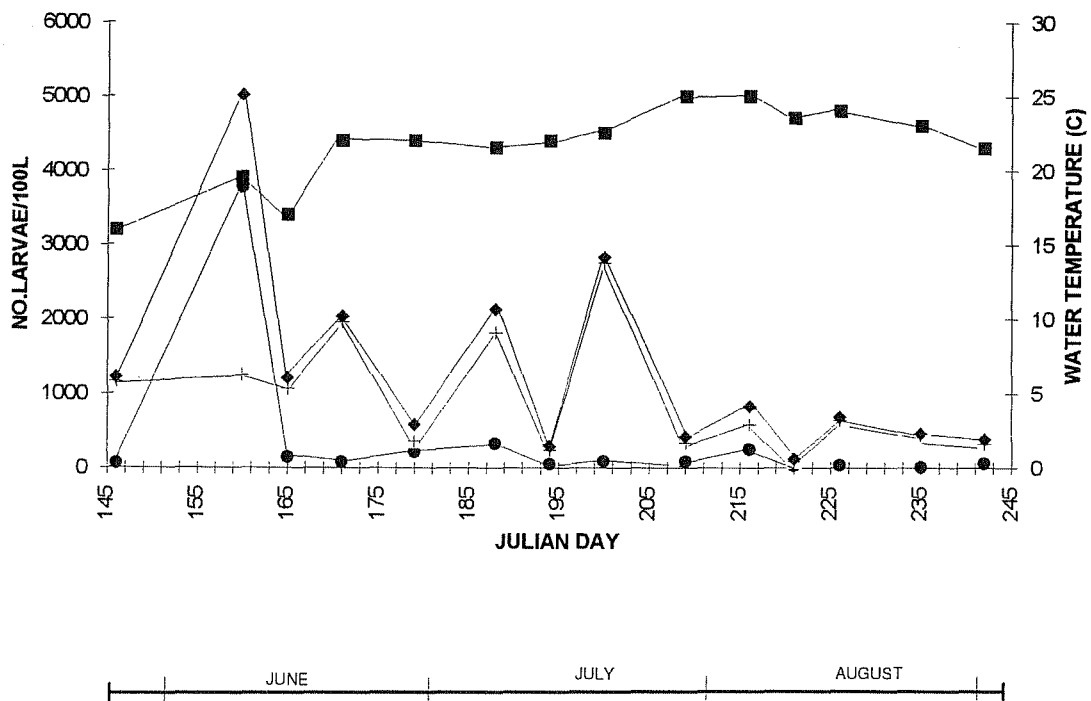


Figure 11. Distribution of bivalve larvae at late stage associated with temperature in Wickford.
—■— : temperature; —●— : quahog larvae; + ; other bivalve larvae; —◆— : total bivalve larvae.

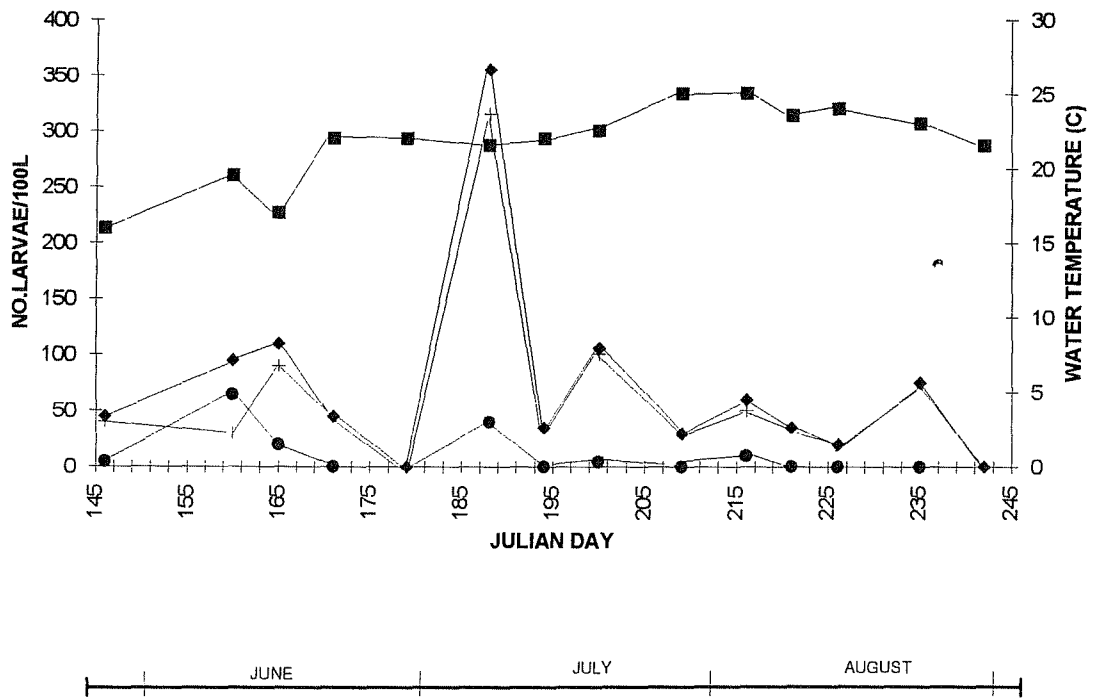


FIGURE 12. Distribution of bivalve larvae associated with moon phase in Narragansett Bay.

—■— : quahog larvae ; —●— : other bivalve larvae; —◆— : total bivalve larvae.

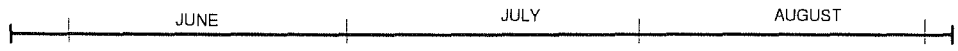
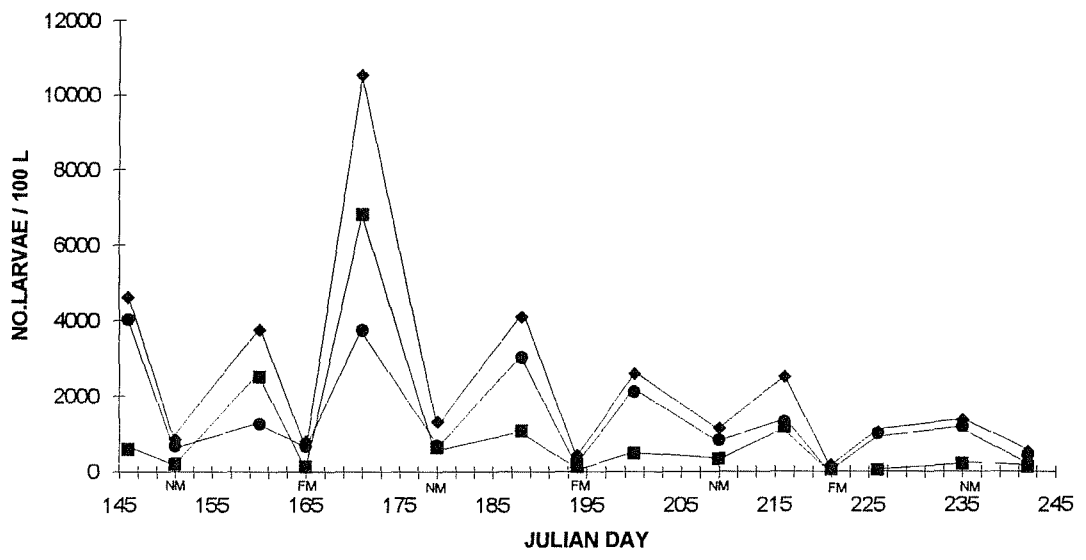


FIGURE 13. Relationship between abundance of quahog larvae and water temperature at Conimicut Pt. during summer 1995.

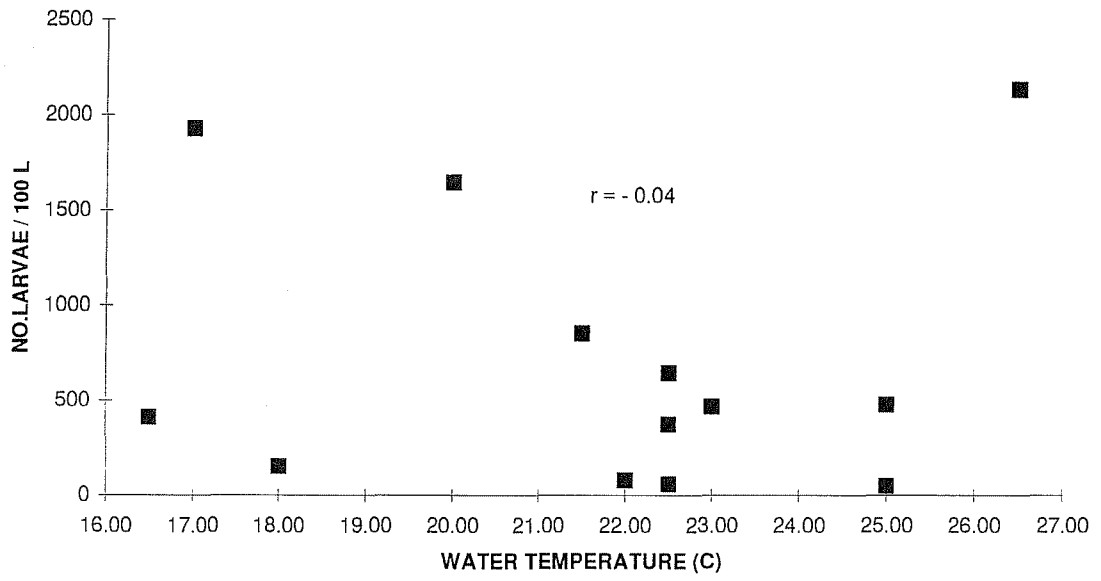


FIGURE 14. Relationship between abundance of quahog larvae and water temperature at Rocky Pt. during summer 1995.

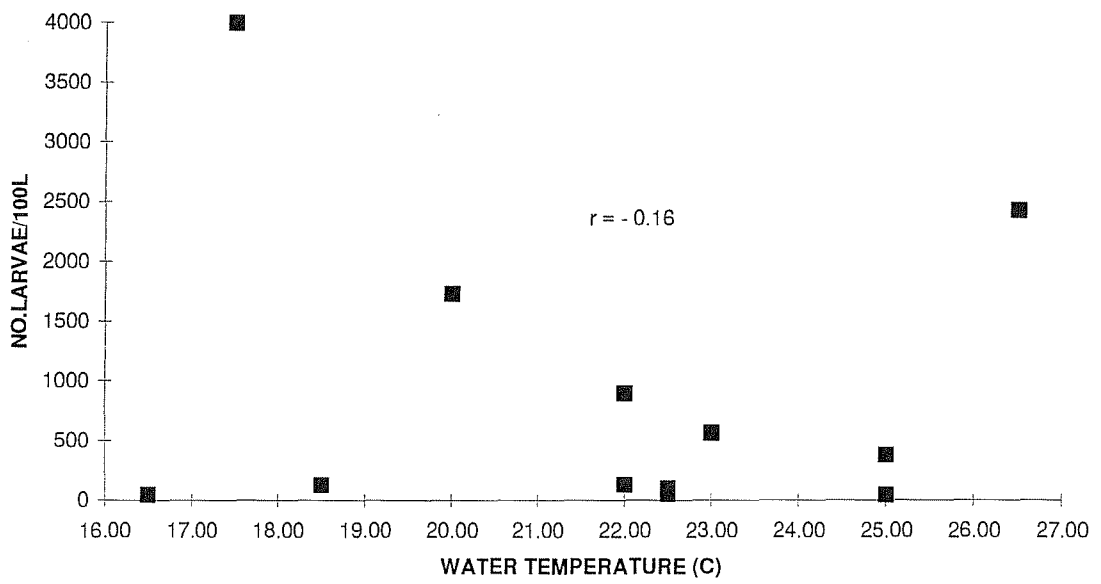


FIGURE 15. Relationship between abundance of quahog larvae and water temperature at Warwick Pt. during summer 1995.

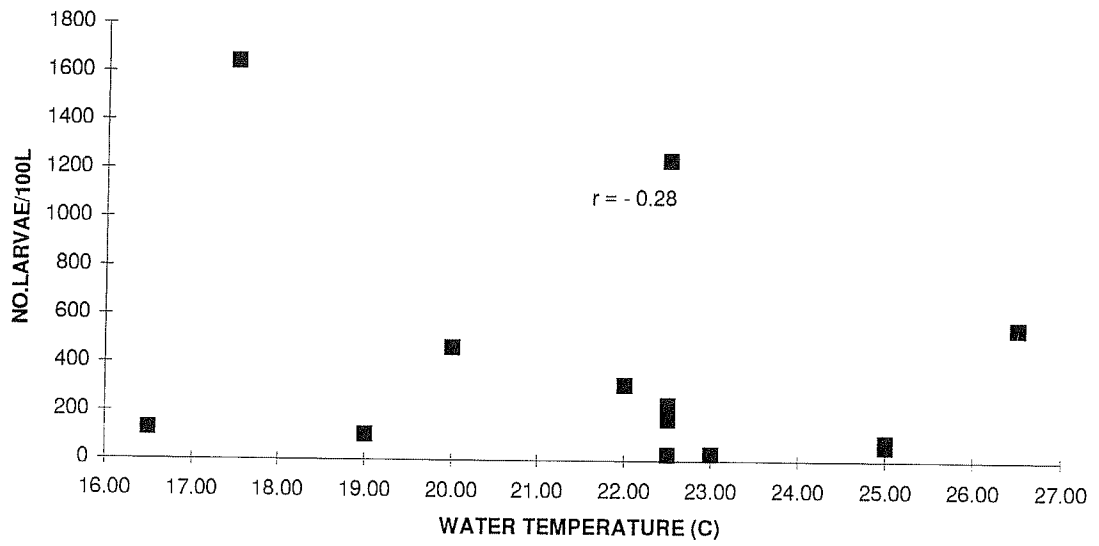


FIGURE 16. Relationship between abundance of quahog larvae and water temperature at Mt. View during summer 1995.

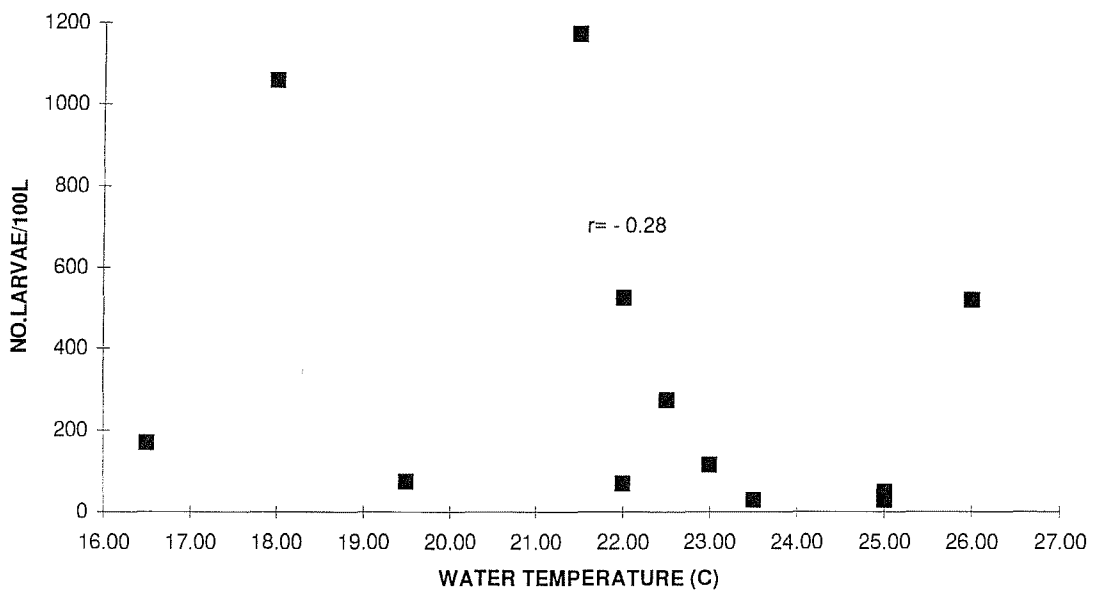
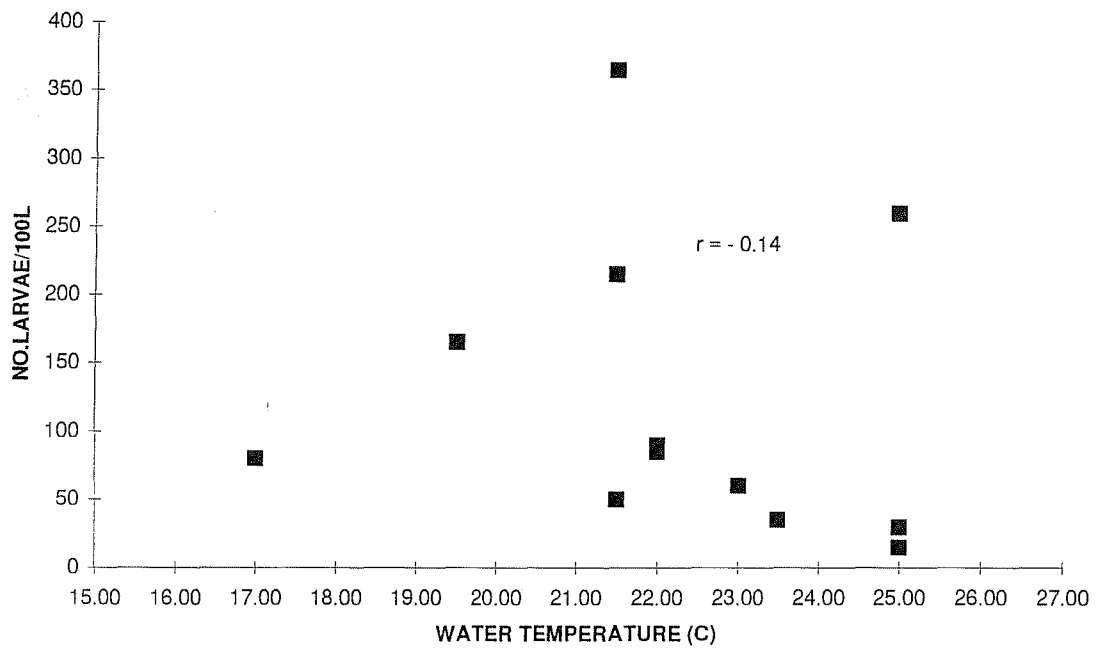


FIGURE 17. Relationship between abundance of quahog larvae and water temperature at Wickford during summer 1995.



DISCUSSION

Distribution of Quahog Larvae

The temporal distribution of quahog larvae may describe the events of the spawning pattern. This study found that quahog larvae at early stage along a North - South transect occurred weekly from May to August. The larvae reached peak abundances on June 20 at all sampling stations, except Wickford. These results are consistent with the results of Landers (1954) and Rice and Goncalo (1995) who reported that peak abundances of bivalve larvae in Wickford and Greenwich Bay occurred on June 11 and on June 14, respectively. The patterns of summer larval abundances indicated that Narragansett Bay quahogs commenced spawning throughout summer months once water temperature rises, and released gametes at least once a week. Intense spawnings, which might relate to major peak abundances of the swarming larvae, could be triggered by increase water temperature to about 20 °C, in mid June.

The reproductive cycle in Narragansett Bay quahogs has been addressed by Diamond (1981). She discovered that two cycles of reproductive activity in quahog population occurred in summer and fall, however, rapid maturation of the gonads which subjects to intense spawning was between April and June. Individuals of this population appear to spawn partially. According to Loosanoff (1937a), an individual quahog does not discharge all of its eggs or sperm at one time, but it continues at intervals of a few days or perhaps weeks to complete the spawning. The male usually spawns first, then stimulates other males and later the females also to spawn (Carriker, 1961). Increased water temperature, coupled with phytoplankton blooming, is considered to be of primary importance

in controlling the spawning (Loosanoff, 1937a, 1937b; Loosanoff and Davis, 1951; Carriker, 1961; Nelson, 1987).

Differences of the temporal pattern of spawning at different sites in a certain estuary may be due to the variations of water temperature. Landers (1954) reported that quahogs inhabiting a shallow water spawned earlier than those in a deeper one. Warming of the exposed bottom in the shallower water triggers release of gametes. This hypothesis may apply in the present study in which that temporal distribution of the larvae in Wickford showed different pattern than in upper bay stations. Both larval stages (i.e., early stage and late stage) in Wickford reached their maximum densities on June 9, earlier than those in other sites. Presumably, there was a major peak of early stages a couple of weeks earlier accounting for the peak of the late stage on June 9. The peak abundances of the larvae in Wickford are likely influenced by the spawner stock inhabiting shallow area. Knowledge of potential excursion of the larvae may facilitate the identification of spawner stock areas in which larvae originate.

Late stage larvae reached peak abundances on July 7 at all sampling stations, except Wickford. If we are to assume that the late stage larvae on July 7 are at the same cohort as the early ones on June 20, then the duration of planktonic life of quahog larvae in Narragansett Bay is about 2 - 3 weeks. According to Loosanoff and Davis (1951), at the age of approximately 12 days or at pediveliger stage, the quahog larvae become competent and ready to settle. We, therefore, can deduce that quahog larvae in Narragansett Bay are ready to settle at least 2 - 3 weeks after fertilization. An intense settlement can occur in the middle of summer as the late stage larvae reached the major peak mostly in July. It appears that once intense settlement occurs, the rate of settlement then gradually declines.

Spawning of bivalves may also coincide with lunar cycles. Intense spawnings of oysters and quahogs and peak abundances of the larvae in Little Egg Harbor occurred concurrently with neap tides (Loosanoff and Nomejko, 1951; Carriker, 1961). During neap tides as tidal amplitude is low, exchange with cooler ocean water results in warmer bay water temperature, thus, inducing intense spawning. On the other hand, high tidal amplitude during spring tides give rise to high tidal exchange which probably accounts for the loss of the larvae. The result of the present study appeared to be consistent with those previous studies that more larvae were observed in the water column during neap tides than during spring tides. Peak abundances of early and late stage larvae occurred coincidentally in neap tides, therein, tidal amplitudes were between 0.55 and 2.2 feet lower than those in spring tides (Chinman and Nixon, 1985; Spaulding et al., 1990).

The second aspect of larval distribution to be discussed is spatial distribution which tends to be patchy and shows a tendency of decreasing number from upper to lower part of Narragansett Bay. In previous studies on plankton dynamics, Smayda (1988) and Durbin and Durbin (1988) reported that bivalve larvae were several fold more abundant in the Providence River and Upper Bay than those in Wickford. The results of the present study were consistent with these. Regardless of the phase of tidal flows, densities of the larvae in Upper Bay stations were always higher, about 1.5 times, than those in Upper West Passage stations. The total bivalve larvae in Upper Bay mostly composed of quahog larvae which decreased in numbers as sampling encountered further down the Bay; while those in Upper West Passage tended to be dominated by larvae of other bivalve species. Presumably, the location of the spawner stock and water circulation of the Bay play an important role in determining this larval dispersion (Carriker, 1951).

According to Okubo (1980, 1994) and Scheltema (1984), the dispersion of the larvae is affected by not only tidal and non-tidal currents but also by turbulent diffusion. Tidal and non-tidal currents, on one hand, are capable of advecting the larvae horizontally from the parent beds. During transport, some of the larvae are trapped in the boundaries (Andrews, 1983; Scheltema, 1984; Okubo, 1994). At the same time, turbulent flow causes the larvae to disperse with respect to one another, giving rise to a distribution in which there is a concentration gradient decreasing from the center of a patch of the larvae outward (Okubo, 1980; Scheltema, 1984). The implication is that fewer numbers of larvae are apparent at increasing distance from the spawner stock beds. Stoner et al. (1996) noted that more queen conch larvae were concentrated in the area near the center of the source of the larvae.

By assuming that those concepts of centroid-like dispersion can be applied to the present study on the distribution of bivalve larvae, the closer the location of the swarming larvae to the spawner stock area, the more the larvae are concentrated in that location. In contrast, the longer the radius of the location of larvae from the parent bed, the less the larvae are found in that location. It, then, appears that Upper Bay is close to the area in which adult quahogs - as the source of the larvae - are abundant. Upper West Passage is likely far from the spawner stock area; although, it might be dominated by communities of other species of bivalve. Thus, by taking Providence River which has been long known being the major spawner stock area of *Mercenaria mercenaria* population as the center of larval dispersion, the concept of centroid-like dispersion might support the data indicating that more quahog larvae stay in Upper Bay since its location is close to Providence River. On the other hand, benthic communities in Upper and Middle West Passage are dominated by *Mulinia lateralis*, *Pitar morrhuana*, and *Macoma tenta* (Sparsis et al., 1993).

Mytilus edulis is also one of the bivalves distributing more in the lower part of the Bay; and the area near Prudence Island is the northernmost region of the occurrence of this species (Nelson, 1984). Therefore, the distribution of bivalve larvae along a North - South transect in Narragansett Bay appears to coincide with adult distribution.

In addition to that, tidal-induced current dominating water circulation is a potential means to displace the larvae from the parent beds, and may contribute to the patchiness of larval dispersion along a longitudinal axis of the estuarine system. Tidal excursion of approximately 1 - 4.4 km in the Bay (Turner, 1984; Spaulding et al. 1990; Turner et al., 1991a, 1991b) is responsible for displacing quahog larvae from Providence River into as far as Upper Bay in one ebb tide, and they can be carried back into the spawner stock area during flood tide. With respect to this phenomenon, it is unlikely that larvae from Providence River can be transported to Upper West Passage, and it seems that there is no free larval exchange between those two areas. Upper layer non-tidal circulation, however, appears to be a supplementary means to advect the larvae beyond the tidal excursion; thus, small numbers of the larvae can be drifted to lower parts of the Bay. It is somewhat difficult to detect the larval transport in this case, unless hydrodynamic model of the Bay and dye studies are performed to explain the process of the transport.

Turner et al. (1991a, 1991b) reported that it took one week for dye released from Providence River to travel into Upper West Passage, a distance of about 20 km. Accordingly, the concentrations of dye declined seaward. Kremer (1975) noted that after two tidal cycles only 2.3 % of the Upper Bay moved into the element Upper West Passage, 6.2 % into Greenwich Bay, 9.7 % into Upper East Passage, 6.2 % into Providence River, and 74 % remains in Upper Bay. The results of those hydrodynamic studies seem to imply that larvae from

Providence River are mostly retained in Upper Bay, and only small fraction of the larvae can be transported into West Passage. In conclusion, it is not surprising that samples of quahog larvae collected during summer 1995 were patchy and more concentrated in upper portions of the Bay.

The effects of filter feeding of adult quahogs may also give a considerable contribution to the patchiness of larval distribution. As a filter feeder, quahogs are able to filter their own larvae (Rice and Goncalo, 1995). As a consequence, densities of the larvae were low in the location in which close to the area of dense adult quahogs (Rice and Goncalo, 1995), and might lead to a relatively high mortality. However, the present study seems not to support their evidence. The possible explanation is that the former study dealt with the area having a shallow depth, while the latter dealt with the area having a deeper depth. The differences of the topography may partly contribute to describe the patchiness of larval distribution due to the effect of benthic predation. Larvae close to or on the bottom are subject to greater predation by filter feeders than those staying in the upper layer (Carriker, 1961). Thus, a study conducted in an area with shallow depths may better represent the real condition of biological interaction on the bottom habitat than the one conducted in the area with deeper depth in which samples collected from upper layer. The depth of the study area within which Rice and Goncalo (1995) conducted sample collections is about 2.0 m. In their study, samples were collected from 0.3 and 1.6 m which are relatively close to the bottom and might well explain the condition of the relation between adult assemblages and larval supply. The average depth of the present study area is approximately 5.6 m (Chinman and Nixon, 1985), and samples were taken from 0.3 and 1.6 m which are considered to be a surface layer.

Mortality

On the basis of the ratio of early and late stage larvae from the same cohort -assumed that the planktonic life is about 2 to 3 weeks-, the mortality of quahog larvae would be between 80 and 99 % (Table 4). This finding seems to be reasonable. Carriker (1961) found only about 2 % of quahog larvae in Little Egg Harbor recruited into the settlement phase and metamorphosis, thus becoming juvenile clams. In Greenwich Bay, Rice and Goncalo (1995) calculated that 95 % of bivalve larvae were lost due to natural mortality.

High mortality at early life stages is common since the animal at this stage is prone to environmental changes and predation. However, quahog larvae are tolerant to a wide range of physical conditions (Carriker, 1961). The quahog larvae may survive in the salinity ranging from 15 to 35 ppt, and in the water temperature between 10 and 30 °C (Carriker, 1961; Davis, 1969). Thus, in a favorable environment which physical condition meets the requirements for survival, the source of quahog larval mortality seems to be due to the predation. There are considerable amounts of predators, which includes adult filter feeders, fish, gastropods, crabs as well as crab larvae (Carriker, 1961; McConaugha, 1985; Rice, 1992).

The larvae of brachyuran crabs are a potential predator of bivalve larvae (Sastry, 1983; McConaugha, 1985). *Pagurus longicarpus* prey upon the oyster veligers (McConaugha, 1985). Laboratory observation showed that *Neopanope texana* is a ferocious predator of young hard clam, however, the predation is considered to be size-dependent (Landers, 1954). In Narragansett Bay, larvae of *Neopanope texana*, *Neopanope sayi*, and *Cancer* spp. were abundant in summer months (Hillman, 1964; Trifan, 1987). During the plankton sampling of summer 1995, there were significant amounts of unidentified crab larvae in the

Bay. Therefore, it is possible that high mortality of quahog larvae during the course of sample collection was partially due to the predation by crab larvae.

Statistical Analyses

Lack of a linear relation between water temperature and larval abundance may be better explained by looking at the nature of the diagram of those variables. A qualitative evaluation shows that the densities of the larvae were low at water temperatures of less than 20 °C. Intense spawning occurred as water temperature rose to 20 °C and was characterized by major peaks of larval abundances. However, the densities then declined following the peak abundances as water temperature increase to above 20 °C. It appears that a water temperature of 20 °C is a threshold to stimulate the spawning, thus, levels of water temperature beyond the threshold give rise to less intense spawning and low larval densities.

Multiple regression analysis showed that only 20 % of the variability of larval abundances can be attributed to the linear model. A large portion of the variability is still left unexplained. Therefore, result of linear correlation and multiple regression analyses suggest that linear model does not seem to be relevant for evaluating the temporal and spatial variations of quahog larvae due to the given physical factors.

SUMMARY

1. Peak abundance of early stage larvae occurred on June 20 (171st Julian day) in all sampling stations, as water temperature reached 20 °C; except in Wickford, the peak occurred 11 days earlier.
2. The peak of late stage larvae occurred 17 days later indicating that the duration of planktonic life is about 2 -3 weeks.
3. The differences in the pattern of larval distribution between upper bay stations and Wickford may be attributed by the variation of spawning biomass distribution, due to the differences in water temperature and distribution of the spawner stock area in which larvae originate.
4. There was a tendency of decreasing gradient of larval abundances from Upper Bay stations to Upper West Passage due to tidal and possibly non-tidal currents.
5. The rate of mortality of quahog larvae was found between 80 and 99 %.
6. The analyses of correlation and multiple regression showed that a linear model only gave little contribution to the variation of quahog larval abundances in Narragansett Bay.

APPENDIX A

Calculation for mortality rate of quahog larvae. E.S, early stage larvae; L.S, late stage larvae.

DAY	LARVAL STAGES	
	E.S	L.S
26-May	573	17
31-May	179	12
9-Jun	2465	29
14-Jun	115	11
20-Jun	6801	10
28-Jun	619	20
7-Jul	963	112
13-Jul	113	12
19-Jul	446	41
28-Jul	318	7
4-Aug	1174	6
9-Aug	44	4
14-Aug	35	6
23-Aug	189	9
30-Aug	111	1

Survival rate of cohort-1 = (L.S on June 9 : E.S on May 26) = 29 : 573 = 0.051

Mortality rate of cohort-1 = 1 - 0.051 = 0.949

Survival rate of cohort-2 = (L.S on June 14 : E.S on May 31) = 11 : 179 = 0.062

Mortality rate of cohort-2 = 1 - 0.062 = 0.938

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Survival rate of cohort-13 = (L.S on Aug 30 : E.S on Aug 14) = 1 : 35 = 0.0286

Mortality rate of cohort-13 = 1 - 0.0286 = 0.9714

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