TEMPORAL DISTRIBUTION OF QUAHOG LARVAE ALONG A NORTH-SOUTH TRANSECT IN NARRAGANSETT BAY, RHODE ISLAND – USA[1]

(Distribusi Temporal Larva Quahog di Narragansett Bay, Rhode Island - USA)

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ABSTRACT

A study on the distribution of quahog (*Mercenaria mercenaria*) larvae in Narragansett Bay, Rhode Island was conducted during a single summer season. Samples of the larvae were collected weekly at five sampling stations distributed landward along the west shore of 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 lunar phase; more larvae were found during neap tides. Early stage larvae, i.e., D-hinge veligers at 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, the 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. In respect to lunar phase, the peak abundances of quahog larvae generally occurred 6 to 12 days after new moon or full moon, coincided with neap tides. 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 occurred in Narragansett Bay around mid July.

Key words: quahog larvae, early stage, late stage, lunar phase, north-south transect.

ABSTRAK

Studi distribusi larva quahog dilakukan selama musim panas di Narragansett Bay, Rhode Island. Pengambilan contoh larva dilakukan setiap minggu pada lima stasiun pengambilan contoh di pesisir barat Rhode Island Sound. Tiga stasiun terletak di bagian atas estuari, yaitu Upper Bay. Sedangkan dua stasiun lainnya berada di bagian bawah estuari, yaitu Upper West Passage. Distribusi temporal quahog larva bersesuaian dengan fasa lunar; larva banyak ditemukan pada saat surut. Larva stadia awal (*D-hinge veliger*) pada umur 1-3 hari muncul setiap minggu selama pengambilan contoh dan kelimpahannya mencapai puncak pada 20 Juni. Kelimpahan larva stadia lanjut (*umbonate veliger*) lebih sedikit dibandingkan dengan stadia awal. Puncak kelimpahan stadia lanjut tersebut ditemukan pada 7 Juli di seluruh stasiun, kecuali satu stasiun. Puncak kelimpahan pada umumnya terjadi 6 – 12 hari setelah bulan baru ataupun bulan purnama, bersamaan dengan terjadinya surut terendah. Berdasarkan puncak kelimpahan kedua stadia perkembangannya, maka dapat diperkirakan bahwa lama hidup larva quahog sebagai plankton adalah sekitar 2-3 minggu. Dengan demikian intensitas penempelan tertinggi larva quahog stadia lanjut kemungkinan terjadi pada pertengahan Juli.

Kata kunci: larva quahog, stadia awal, stadia lanjut, fasa lunar, transek utara-selatan.

INTRODUCTION

The Quahog Fishery

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; and 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 e*t 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).

Despite many studies focusing on the adult quahog populations (Stickney and Stringer, 1957; Saila *et al*., 1967; Jones *et al*., 1989; Rice *et al*., 1989), there have been few studies on quahog larvae in Narragansett Bay. Landers (1954) 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 1995 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 temporal pattern of quahog larval distribution in the western part of Narragansett Bay.

Ecobiology of Quahog Larvae

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 hermaphrodism (Rice, 1992). Spawning normally begins in the late spring as water temperature increases (Menzel, 1989; Rice, 1992), and it lasts into the summer months (Bricel, 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 trochopore larva. At an age of 1-3 days, a velum develops to facilitate swimming. At this stage, a 90-140 μm straight-hinge is form at the dorsal section of the valves. Thus, it is called a straight-hinge 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.

On the studies of oyster larvae near Oŏsterschedel, 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 abundances of the larvae showed minor peaks in the intervening periods.

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 $^{\circ}$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 abundances in Little Egg Harbor, New Jersey. However, in his study of oyster larvae near Oŏsterschedel, Holland, Korringa (1947) attempted to show but failed to prove that the peak of larval abundance depends upon water temperature.

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) Mortality rate at early life stages of quahog would be higher than 90 %.

MATERIALS AND METHODS

Study Area

Narragansett Bay is a major estuary in Rhode Island; and considered as the largest one in southern New England. Its location is sur-

rounded by four coastal areas: Long Island Sound, Block Island Sound, Rhode Island Sound, and Buzzard's Bay (Spaulding, 1987). The Bay is 40 km in length (Gordon, 1982); the surface area, shoreline length, and mean water volume are about 328 km^2, 412.5 km, and 2,724 km^3, respectively (Chinman and Nixon, 1985; Spaulding, 1987). Mean water depth is 8.3 m (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 rives discharge into the Providence River, while the last one empties into Mount Hope Bay (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 (Pilson, 1985). Salinity decreased from the entrance to the head of the Bay; 31 g/kg at the entrance, while at the head values in the range of 10-20 g/kg (Hicks, 1959). 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). The most northerly station, Connimicut Pt. (41° 43'), was located approximately 500 m southeast of Connimicut Point. The second station is Rocky Pt. (41° 41.5') which was about 500 m in front of Rocky Point amusement park shore. Warwick Pt. (41° 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° 38') which was about 4 km south of the mouth of Greenwich Bay and Wickford (41° 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, from May 26 to August 30.

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 (!971). The quahog larvae were categorized into two developmental stages, the early stage or straight-hinge larvae and the late stage or umbonate stage.

Enumeration of Larvae

Number of larvae per 100 liter water samples (*N*) were calculated:

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

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

$$S = \frac{N_{t+1}}{N_t} \qquad (2)$$

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:

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

Statistical Analyses

A Wilcoxon Rank-Sum Test was used to examine the abundances of quahog larvae during neap tides vs spring tides (Johnson and Bhattacharya, 1992). The procedure is as follow: 1) Assign H_0: larval abundances during neap tides and during spring tides are identical. 2) Rank the combined value of $n = n_A + n_B$ observations in the increasing order of magnitude. n_A = numbers of larvae during neap tides; n_B = number of larvae during spring tides. 3) Find the rank sum W_A of the first sample having smaller sum of the ranks. 4) Assign H_1: those two abundances are different. 5) Assign R: $p = P\left(W_A \leq x^*\right) = P\left(W_A \geq x\right)$.

RESULTS

Physical Environment

Data of surface water temperature is presented in Table 1. Water temperature measured 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.

Distribution of Larvae

Temporal distributions of *Mercenaria mercenaria* larvae, at early and late stages, are illustrated in Figures 1 to 5. 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.

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 per100 l) occurred 11 days earlier (June 9) than that at other stations, where water temperature was only 19.5 °C when the peak occurred. Abundance, afterward, were less than 325 larvae per 100 l.

Table 1. Temperature (°C) at Five Sampling Stations in Narragansett Bay.

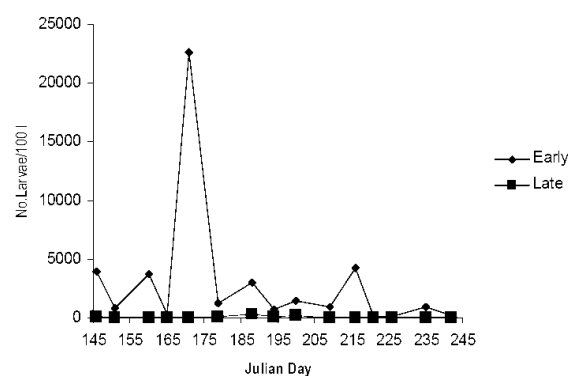| Julian Day	Conimicut Pt	Rocky Pt.	Warwick Pt.	Mt. View	Wickford
146	16.5	16.5	16.5	16.5	16.0
151	17.0	17.5	17.5	18.0	N/A
160	18.0	18.5	19.0	19.5	19.5
165	17.0	17.0	16.5	17.0	17.0
171	23.0	22.0	23.0	22.0	22.0
179	20.0	20.0	20.5	21.5	22.0
188	22.5	22.5	23.0	22.0	21.5
194	21.5	22.0	22.0	22.5	22.0
200	22.5	22.5	23.0	23.5	22.5
209	26.5	26.5	26.5	26.0	25.0
216	25.0	25.0	25.0	25.0	25.0
221	22.5	22.5	22.5	23.5	23.5
226	24.0	24.0	24.0	23.5	24.0
235	22.0	22.0	22.5	23.0	23.0
242	21.0	21.0	21.5	22.0	21.5

N/A: not available

Figure 1. Densities of Quahog Larvae at Early and Late Stages in Conimicut Pt.
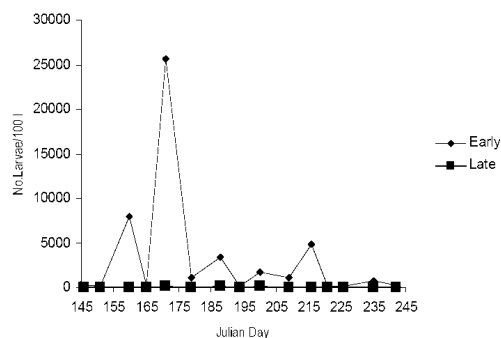
Figure 2. **Densities of Quahog Larvae at Early and Late Stages in Rocky Pt.**
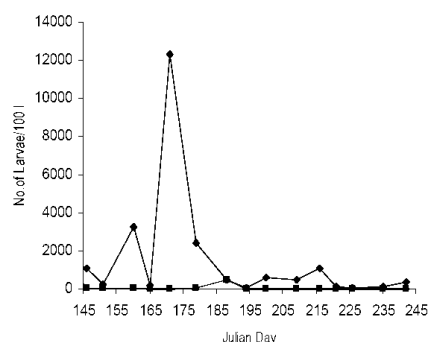

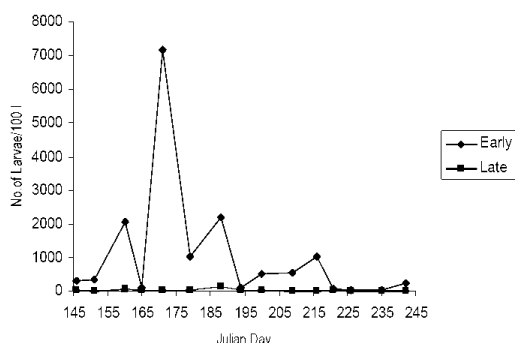**Figure 3.** **Densities of Quahog Larvae at Early and Late Stages in Warwick Pt.**

Figure 4. **Densities of Quahog Larvae at Early and Late Stages in Mt. View.**
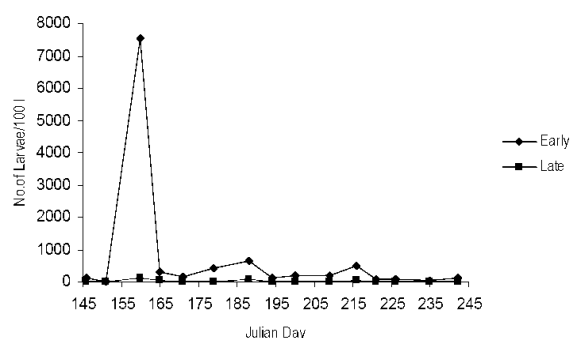

Figure 5. **Densities of Quahog Larvae at Early and Late Stages in Wickford.**

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 6). 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.
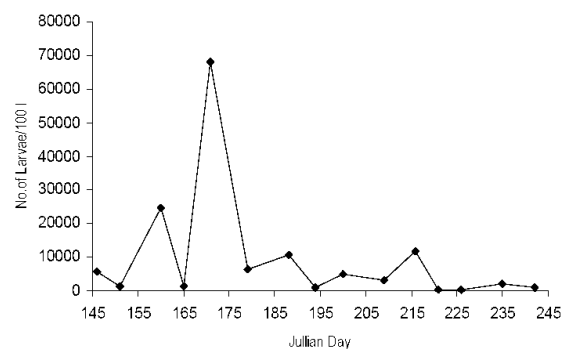

Figure 6. Distribution of Quahog Larvae in Narragansett Bay.

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 2 shows the rate of mortality of quahog larvae in Narragansett Bay which ranged from 80 to 90%.

Table 2. **Rate of Mortality of Quahog Larvae in Narragansett Bay During Summer.**

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

Statistical Analyses

A non parametric procedure utilized for comparing larval abundances in neap and spring tides demonstrated a significant difference.

DISCUSSION

Temporal 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 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 ºC, 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 week to complete the spawning. The male usually spawn 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 spawn-ing (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 in-habiting 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 stage 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 assumed 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 coinciden-

tally 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).

Mortality

On the basis of the ration 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 to 99 % (Table 2). 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 g/kg, and in the water temperature between 10 and 30 $^{\circ}$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 sized-dependent (Landers, 1954). In Narragansett Bay, larvae of Neopanope texana, Neopanope say, 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

A significant difference on a non parametric procedure, utilized for comparing larval abundances in neap and spring tides, supports previous studies (Korringa, 1947; Carriker, 1961) which reported that the abundances of bivalve larvae were different during neap and spring tides.

CONCLUSION

Generally, the quahog larvae tended to invade water column as water temperatures got warmer in all stations but one, i.e., Wickford.

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. 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 larvae at Wickford, however, showed different pattern. The maximum abundance (3,775 larvae per100 l) occurred 11 days earlier (June 9) than that at other stations. 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 concentrateion 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).

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. Thus, rate of mortality of quahog larvae in Narragansett Bay ranged from 80 to 90 %.

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