

# LIFE TABLES FOR TWO FIELD POPULATIONS OF SOFT-SHELL CLAM, *MYA ARENARIA*, (MOLLUSCA : PELECYPODA) FROM LONG ISLAND SOUND

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## ABSTRACT

Life tables were constructed for two populations of *Mya arenaria* from Long Island Sound, USA, based on schedules of age-specific fecundity and mortality determined under natural conditions. *Mya arenaria* shows a basic conservatism in general life history pattern. In both populations, fecundity increases with increasing female size; sexual maturity is attained at 1 year of age; a single annual breeding season occurs and survivorship curves approximate the type III of Deevey, which is characterized by extremely heavy mortality early in life followed by relatively constant mortality thereafter. Differences in the age-specific parameters for the two populations exist, however; for clams greater than 1 year of age, both age-specific fecundity and survivorship are significantly higher in the Stonington population. These differences in the structure and dynamics of the two populations may be due to environmental heterogeneity. Reduced body size due to slower growth in coarse substrate, as well as the increased maintenance demands resulting from burrowing and valve activity in large-grained sediment, may account for the lower egg production and lower survival rates found in the Westport population.

The life history pattern of a species has been defined as the way in which that species partitions the limited resources of time or energy among the three basic biological processes of growth, maintenance, and reproduction. Efforts to generate empirical values for life history parameters, age-specific fecundity and survivorship, have only recently allowed the construction of life tables for field populations. Determining life history parameters for a commercially important species such as the soft-shell clam, *Mya arenaria*, is particularly useful since they can be used in theoretical models which are designed to analyze the effect of changing survival and fecundity values on the growth rate of the population.

Life tables now exist for a number of benthic marine invertebrates: the barnacle—*Chathamulus stellatus* (Connell 1961); the prosobranchs—*Dicathais orbita* (Phillips and Campbell 1974), *Nucella* (= *Thais*) *lapillus* (Frank 1969), *Nodilittorina tuberculata* (Doran 1968), and *Comus penanceus* (Perron 1983); the coelenterates—*Muricea californica* (Grigg 1977), *M. fruticosa* (Grigg 1977), and *Balanophyllia elegans* (Fadlallah 1983); the bivalves—*Mya arenaria* (Brousseau 1978), *Tapes phillipinarum* (Yap 1977), and *Gemma gemma*

(Weinberg 1985). These studies, however, examine life history parameters for a single species population or for successive cohorts within a population.

The present study examines age-specific fecundity and survivorship in two geographically separated populations of the soft-shell clam, *Mya arenaria*, using identical methodology. Since differences in methodology can influence estimates of demographic parameters (Fadlallah 1983) uniformity of approach is necessary for interpopulation comparisons. This study is the first reported examination of species-specific traits in two naturally occurring populations and was carried out as part of a broader study of the population dynamics of this species along the Connecticut shore of Long Island Sound.

## MATERIALS AND METHODS

### Field Study Areas

Field studies were conducted at two intertidal sites in Long Island Sound, one located at Barn Island in Stonington, CT (lat. 41°20'N; long. 71°53'W) and the other in the Saugatuck River in Westport, CT (lat. 41°06'N; long. 73°23'W) (Fig. 1). The Stonington site is a narrow intertidal sandflat which extends approximately 10 m shoreward to a coarse sand beach. At low tide the Westport site extends 30 m (at its widest point) shoreward to a *Spar-*

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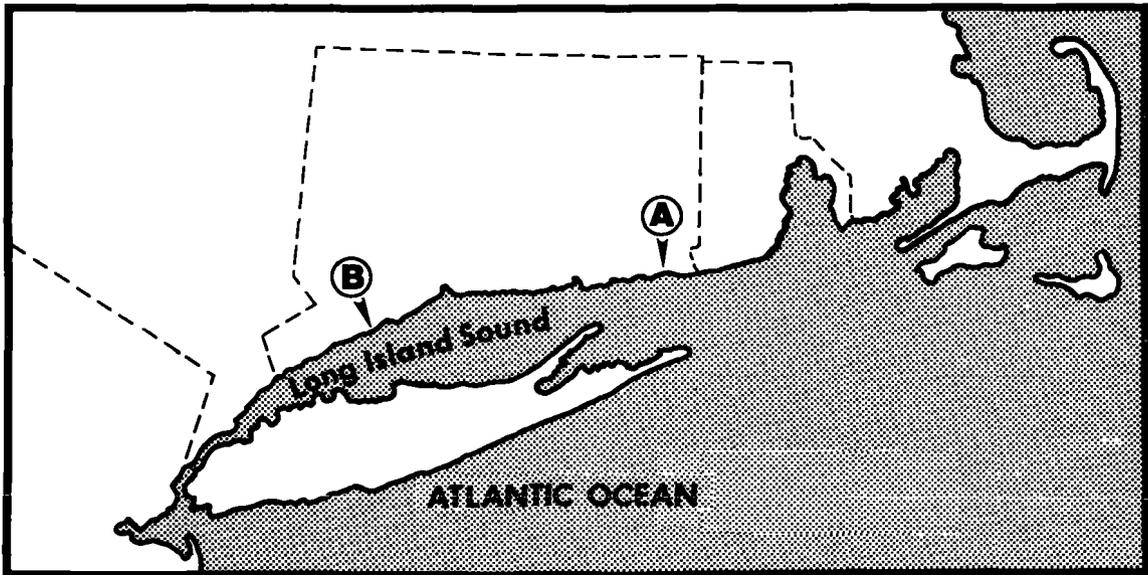


FIGURE 1.—Map showing locations of the two study sites: Barn Island in Stonington, CT (A) and Saugatuck River in Westport, CT (B).

*tina alterniflora* marsh. The substrate there is coarser than at the Stonington site; 50% by weight is >4 mm grain size diameter, much of that classifiable as either cobble or boulder (Brousseau and Baglivo 1987). Both study sites are closed to shellfish harvesting to high levels of bacterial contamination.

Although annual salinity and temperature profiles for the two sites are not available, monthly surface and bottom salinity and temperature readings for the period March 1979–June 1981 and October 1985–August 1986 are available for four sites in western Long Island Sound: Norwalk, CT (lat. 41°02.5'N; long. 73°27.2'W), Bridgeport, CT (lat. 41°08.7'N; long. 73°11.1'W), Stratford, CT (lat. 41°07.6'N; long. 73°07.6'W), and New Haven, CT (lat. 41°14.4'N; 72°54.2'W) (Tettlebach et al., 1984; Blogoslawski, pers. comm.<sup>3</sup>). All water sampling was done at spring low tide in approximately 20 ft of water. The annual average range of surface temperatures for the four sites was 0.5°–24.2°C. The lowest surface temperature, 0.0°C, was recorded at the New Haven station in February 1980; the highest was 25.0°C recorded at the Stratford station in August 1986. Annual average range of bottom temperatures was 0.6°–23.4°C. Surface salinities ranged from 16.9 to 33.3‰ with a low of 15.9‰

reported for Stratford and a high of 35.7‰ recorded at the Norwalk station. Mean bottom salinities during that period ranged between 17.0 and 34.4‰.

### Fecundity

Oocyte production by female clams collected during the summer spawning seasons of 1984 and 1985 was estimated using a histological technique (Brousseau 1976). One hundred twenty-five gravid females from the Westport population and 123 from the Stonington population were examined. Size-specific fecundity rates were converted to age-specific rates using age-size information for *M. arenaria* obtained from analysis of internal shell growth bands (Brousseau and Baglivo 1987). Age-specific fecundity estimates for  $x$ -yr-old clams,  $m_x$ , were calculated using the formula:

$$m_x = 0.5 \sum m_i P(\text{size-class } i \mid x \text{ yr-old}) \quad (1)$$

where  $m_i$  is the mean fecundity for size-class  $i$ ,  $P(\text{size-class } i \mid x \text{ yr-old})$  is the conditional probability that an  $x$ -yr-old clam is in size-class  $i$ , and the sum is taken over 10 mm size-classes  $i$ . The conditional probabilities  $P(\text{size-class } i \mid x \text{ yr-old})$  were derived empirically (see Appendix Tables 1, 2). Ten millimeter size-classes were used because of sparseness in the data. By convention,  $m_x$  represents the

<sup>3</sup>W. Blogoslawski, Northwest Fisheries Center Milford Laboratory, National Marine Fisheries Service, NOAA, Roger Avenue, Milford, CT 06460, pers. commun. March 1987.

total number of eggs produced by a female of age  $x$  which may be considered to be "female eggs". Because the sex ratio of both populations is 1:1 (Brousseau 1987a), only half of the oocytes produced will eventually become females. Accordingly, each  $m_x$  is one-half the total annual fecundity per female of age  $x$ .

### Mortality

To determine size-specific 1-yr survival rates of adult clams (>1 year of age), *M. arenaria* from Stonington and Westport were collected, individually tagged, and returned to their original sites (Stonington: 31 May–1 June 1985; Westport (Plot A): 1 May 1984 and Westport (Plot B): 22 May 1984). Clams were measured to the nearest 0.1 mm antero-posteriorly and marked for identification using a method described previously (Brousseau 1979). Tagged clams were replanted in parallel furrows excavated to a depth of 20–30 cm. All plots were 0.3 m apart and located at midtide level (+3.0 m). At the end of the test period, the clams were collected. All numbered individuals, both alive and dead, were returned to the laboratory for measurement. A total of 1,049 clams from the Stonington population were tagged, of which 78% were recovered. One-year recovery rate at the Westport site was 40% of the 1,977 clams initially planted. Mortality rates were determined on the basis of the number of clams recovered. This method gives a more accurate estimate of mortality since it does not consider clams that were not recaptured in these estimates.

If, on recapture, a dead clam showed no evidence of growth, either death had occurred naturally in a slow-growing individual or premature death had occurred as a result of trauma due to the marking procedure. In order to correct for premature mortality caused by handling, the proportion of live clams which showed an increase in shell length over the year was calculated (Table 1). For the Westport population all live clams <40 mm shell length grew, while 94.7% of live clams over 40 mm grew. For the Stonington population all live clams <50 mm shell length had grown during the year, while 91.9% of

live clams over 50 mm grew. In order to estimate size-specific survivorship then, the following rules were applied:

#### Westport:

$$\text{Classes } <40 \text{ mm: } P(\text{surviving one year}) \quad (2)$$

$$= N_A / (N_A + N_{DG})$$

$$\text{Classes } >40 \text{ mm: } P(\text{surviving one year})$$

$$= N_A / (N_A + N_{DG}/0.947)$$

#### Stonington:

$$\text{Classes } <50 \text{ mm: } P(\text{surviving one year}) \quad (3)$$

$$= N_A / (N_A + N_{DG})$$

$$\text{Classes } >50 \text{ mm: } P(\text{surviving one year})$$

$$= N_A / (N_A + N_{DG}/0.919)$$

where  $N_A$  is the number alive and  $N_{DG}$  is the number dead with growth. In the smaller classes (Westport, <40 mm; Stonington, <50 mm), the sum  $N_A + N_{DG}$  represents all recovered individuals, while in the larger classes, the adjustment factor allows us to add a number of dead without growth back into the total recovered in the same proportion as the live with no growth.

Age-specific survival rates,  $P_x$ , were based on the same age-size information used to determine age-specific fecundity rates. These rates were calculated using the formula:

$$P_x = \sum p_i P(\text{size-class } i \mid x\text{-yr-old}) \quad (4)$$

where  $p_i$  is the probability that a clam in size-class  $i$  survives one year,  $P(\text{size-class } i \mid x\text{-yr-old})$  is the conditional probability that an  $x$ -yr-old clam is in size-class  $i$ , and the sum is taken over 10 mm size classes  $i$ .

The probability of surviving from settlement to one year (a period of about 10 months) is calculated from the estimates of the density of the population in 2 consecutive years. Both populations were sampled during periods of maximum settlement in 1985. This period occurred approximately 3 weeks earlier in the Westport population. At each sampling, 18 to 35 samples (0.1 m<sup>2</sup> × 30 cm deep) were taken along transects running from mean low water shoreward to the mean high water mark. Samples were wet-seived in the laboratory (2 mm mesh) and the shell lengths of the clams retained by the seive were measured. Clams of size 2–20 mm in the first year of sampling are assumed to be the spat; those of size 20–50 mm the following year are assumed to have come proportionately from the settlement of the previous year in the same ratios as the empirical probability distributions (Appendix Tables 1, 2).

TABLE 1.—Distribution of *Mya arenaria* recovered alive showing growth and no growth during the test period.

	Westport (clams >40 mm)		Stonington (clams >50 mm)	
	Growth	No growth	Growth	No growth
Number	196	11	440	39
Percent	94.7	5.3	91.9	8.1



TABLE 2.—Densities per 0.1 m<sup>2</sup> of *Mya arenaria* in size-classes 2–50 mm in the Westport and 2–60 mm in the Stonington populations in 1985 and 1986.

Location and date	Samples	Size-class (mm)	N/0.1 m <sup>2</sup>	(range)
<b>Westport, Connecticut</b>				
23 July 1985	28	2–20	23.36	(0–84)
09 June 1986	18	10–20	0.11	(0–1)
		20–30	0.44	(0–5)
		30–40	0.89	(0–4)
		40–50	0.50	(0–3)
<b>Stonington, Connecticut</b>				
15 Aug. 1985	35	2–20	0.37	(0–7)
24 June 1986	24	20–30	0.04	(0–1)
		30–40	0.13	(0–1)
		40–50	0.33	(0–2)
		50–60	0.75	(0–3)

period (10 months) obtained by dividing the number of 1-yr-olds alive in the summer 1986 by the estimated cohort size in the previous year were 0.0283 and 0.5869 for the Westport and Stonington populations, respectively.

Size-specific survival rates of adult clams (≥1 year) at both sites are shown in Tables 3 and 4. These represent empirical estimates from mark and recapture studies with survival adjustments in the larger classes made according to Equations (2) and (3). Statistical comparison of the survival distributions of adult clams, however, was limited to those recovered live or recovered showing some growth. At the Westport site survival was constant across the 10 mm size classes: 20–29 through 50–59 and 60+. At Stonington, however, the size-specific survival for classes 30–39 through 70–79 and 80+ increased slightly with size ( $P < 0.05$ ,  $\chi^2$  test). The probability

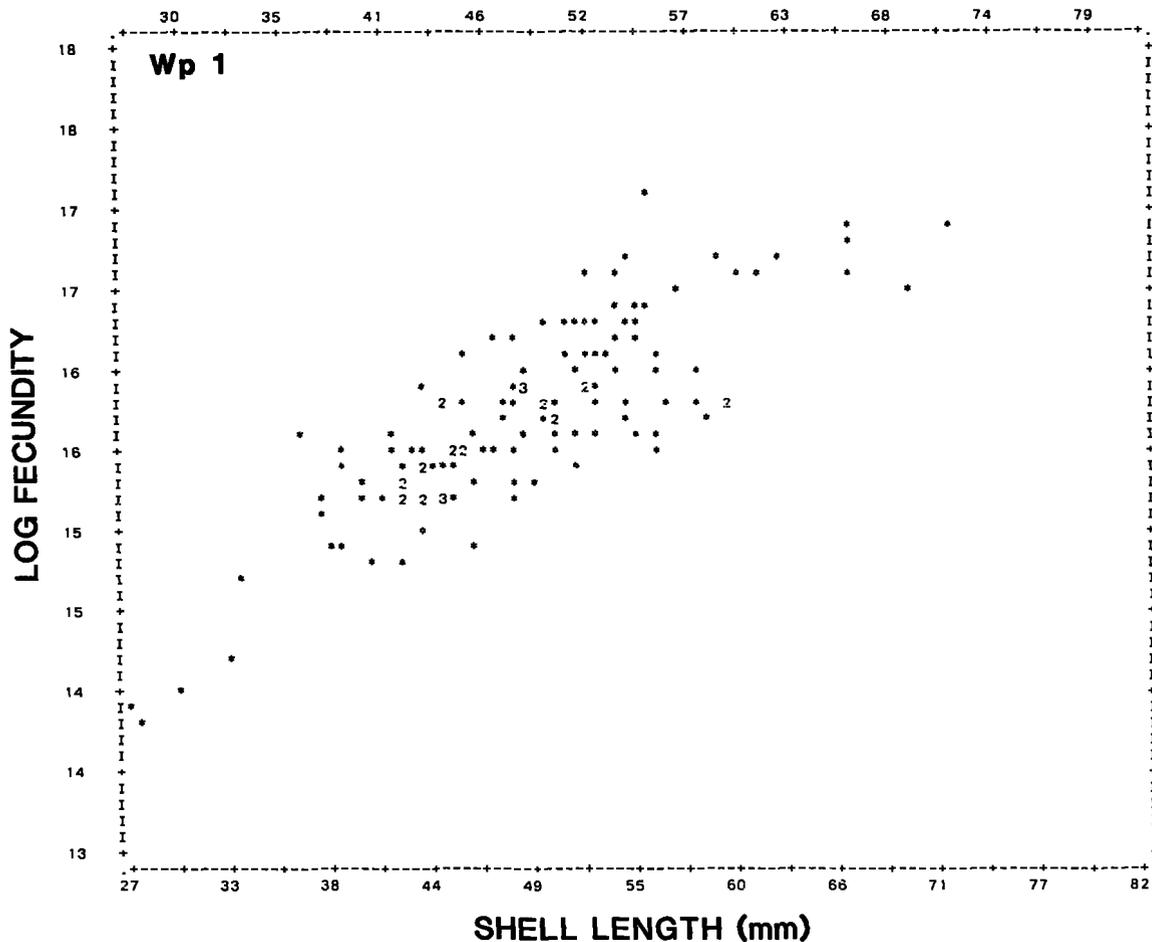


FIGURE 2.—Continued—the Stonington (STN) and Westport (WP1) populations.

TABLE 3.—Size-specific survival rates for marked *Mya arenaria* from the Stonington population.  $P$  = probability of an individual from size-class  $i$  surviving one year;  $N_A$  = number of live clams;  $N_{DG}$  = number of dead clams showing growth.

Size-class	Size (mm)	$N_A$	$N_{DG}$	$P$
2	20–30			
3	30–40	23	3	0.8846
4	40–50	106	18	0.8548
5	50–60	134	7	0.9462
6	60–70	161	11	0.9308
7	70–80	159	9	0.9420
8	80+	25	0	1.0000

TABLE 4.—Size-specific survival rates for marked *Mya arenaria* from the Westport population.  $P$  = probability of an individual from size-class  $i$  surviving one year;  $N_A$  = number of live clams;  $N_{DG}$  = number of dead clams showing growth.

Size-class	Size (mm)	$N_A$	$N_{DG}$	$P$
2	20–30	15	5	0.7500
3	30–40	87	56	0.6084
4	40–50	150	76	0.6515
5	50–60	48	19	0.7052
6	60–70	9	5	0.6303
7	70–80	0	0	0.0000
8	80+			

of surviving one year for adult clams at Stonington (30+ mm in shell length) is significantly higher than at Westport (20+ mm in shell length) ( $P < 0.001$ ,  $\chi^2$  test).

Age-specific survivorship estimates (Table 5) were calculated by assuming that 20–30 mm clams at Stonington survived with the same probability as 30–40 mm clams and that 90–100 mm clams at Stonington survived with the same probability as 80–90 mm clams and application of Equation (4) using the empirical distributions in Appendix Tables 1 and 2.

TABLE 5.—Age-specific survival rates for marked *Mya arenaria* from the Westport and Stonington, CT populations.  $P_x$  = probability of surviving from age-class  $x$  to age-class  $x + 1$ .

Age-class (yr)	Westport $P_x$	Stonington $P_x$
1	0.6390	0.8843
2	0.6442	0.9307
3	0.6625	0.9390
4	0.6680	0.9550
5	0.6595	0.9661
6	0.6422	0.9746
7	0.6128	0.9746
8	0.5991	0.9746
9	0.5021	0.9746

## Population Dynamics

The age-specific survivorship and fecundity schedules for *M. arenaria* are combined in life table form in Tables 6 and 7. Since rates of larval survivorship are difficult to measure for species with planktonic larvae, simplifying assumptions are necessary for estimating survivorship probabilities of larvae (age 0). In order to complete the life tables the equilibrium settlement rates ( $r_s$ ) were calculated using the method of Brousseau et al. (1982). Our choice of  $r_s$  implies that the net reproductive rate,  $R_0$ , which is defined by  $R_0 = \sum l_x m_x$ , were  $l_x$  = survivorship and  $m_x$  = fecundity, equals one for both populations. This is not meant to imply however, that the populations studied here are considered to be in equilibrium. Rather, it is used simply as a theoretical construct in which to examine possible consequences of differing fecundity and mortality schedules on the two populations of *M. arenaria*.

TABLE 6.—Life table for the Westport, CT *Mya arenaria* population, assuming equilibrium conditions.  $l_x$  = survivorship to beginning of age interval  $x$ , or  $l_{x-1} \times P_{x-1}$  when  $x > 1$ ;  $m_x$  = fecundity during age interval  $x$ .

Age (yr)	$l_x$	$m_x$	$l_x m_x$
0	1.0		
1	$1.0599 \times 10^{-7}$	1485615	0.1575
2	$6.7728 \times 10^{-8}$	2989512	0.2025
3	$4.3630 \times 10^{-8}$	3867846	0.1688
4	$2.8905 \times 10^{-8}$	5192053	0.1501
5	$1.9309 \times 10^{-8}$	5892286	0.1138
6	$1.2734 \times 10^{-8}$	6464925	0.0823
7	$8.1780 \times 10^{-9}$	6478050	0.0530
8	$5.0115 \times 10^{-9}$	6842903	0.0343
9	$3.0024 \times 10^{-9}$	8390977	0.0252
10	$1.5075 \times 10^{-9}$	8390977	0.0126

<sup>1</sup> $l_1 = r_s \times$  (probability of surviving from 2 months to 1 year).

TABLE 7.—Life table for the Stonington, CT *Mya arenaria* population, assuming equilibrium conditions.  $l_x$  = survivorship to beginning of age interval  $x$ , or  $l_{x-1} \times P_{x-1}$  when  $x > 1$ ;  $m_x$  = fecundity during age interval  $x$ .

Age (yr)	$l_x$	$m_x$	$l_x m_x$
0	1.0		
1	$1.2014 \times 10^{-8}$	1109952	0.0224
2	$1.7811 \times 10^{-8}$	3712746	0.0661
3	$1.6577 \times 10^{-8}$	4947569	0.0820
4	$1.5566 \times 10^{-8}$	7125027	0.1109
5	$1.4866 \times 10^{-8}$	8287563	0.1232
6	$1.4362 \times 10^{-8}$	8724158	0.1253
7	$1.3997 \times 10^{-8}$	8724158	0.1221
8	$1.3642 \times 10^{-8}$	8724158	0.1190
9	$1.3296 \times 10^{-8}$	8724158	0.1160
10	$1.2958 \times 10^{-8}$	8724158	0.1130

<sup>1</sup> $l_1 = r_s \times$  (probability of surviving from 2 months to 1 year).

The equilibrium settlement rate ( $r_s$ ) for the Westport population is  $3.7453 \times 10^{-6}$  and that for the Stonington population is  $3.4318 \times 10^{-8}$ . The equilibrium first year survival rates (i.e., the probability of surviving from egg to year 1 necessary to maintain a population at equilibrium) then, become  $1.0599 \times 10^{-7}$  and  $2.014 \times 10^{-8}$  for the Westport and Stonington populations, respectively.

Under the assumption of equal rates of larval import and export, it is possible to calculate empirical settlement rates by estimating the total number of eggs released per unit area by spawning females in 1985 and dividing this value into the densities of 2–20 mm spat settled per unit area 2 months later. Size-frequency data for the populations was used to determine the number of clams in each 10 mm size class (Fig. 3). The number of animals in each class (assuming that one-half the population is female) was multiplied by the mean size-specific annual fecundity value for that size class. Summing over all size classes of reproducing females gives an estimate of the 1985 oocyte production per unit area. Empirical settlement rates of  $8.4589 \times 10^{-6}$  and  $7.1953 \times 10^{-8}$  were calculated for the Westport and Stonington populations. These represent values of 2.2585 and 2.0967 times the estimated equilibrium settlement rate of these populations. Multiplying the empirical settlement rate by the probability of surviving the remainder of the year give actual first year actual first year survival rates of  $2.3939 \times 10^{-7}$

and  $4.2229 \times 10^{-8}$  for Westport and Stonington, respectively.

The heavy mortality evident by the low juvenile survivorship rates ( $l_1$ ) for *M. arenaria* take into account the losses incurred during fertilization, metamorphosis and recruitment, and subsequent survival through the first year of life. Table 8 compares the first year survival rates of representative marine invertebrate species with planktonic and nonplanktonic modes of development. Early survival in species lacking planktonic larvae is on average, three orders of magnitude higher than that of species which pass through a planktonic larval stage.

## DISCUSSION

General comparisons of life history traits are useful but quantitative comparisons are possible only from the more detailed information found in life tables (age-specific fecundity and survivorship). The difficulty in generating such information, especially for marine bivalves, many of which have planktonic larval stages during their life cycles, has resulted in the construction of few complete life tables. Moreover, no reported field study has examined life history traits for more than one population of a species simultaneously. Consequently, the extent to which quantitative differences in life history parameters are characteristic of the life history of a single species is unknown.

TABLE 8.—Empirical estimates of first year survival rates of marine invertebrate species with and without planktonic larvae (adapted from Perron 1983).

Class	Species	Survivorship $l_1$	Developmental mode	References
Anthozoa	<i>Muricea californica</i>	$2.6 \times 10^{-7}$	planktonic	Grigg (1977)
	<i>Muricea fruticosa</i>	$3.7 \times 10^{-6}$	planktonic	Grigg (1977)
	<i>Balanophyllia elegans</i>	$5.0 \times 10^{-2}$	nonplanktonic	Fadlallah (1983)
Bivalvia	<i>Gemma gemma</i> Cohorts 1978–1981	$2.3 \times 10^{-2}$ $1.2 \times 10^{-1}$ $2.0 \times 10^{-1}$ $1.1 \times 10^{-1}$	nonplanktonic	Weinberg (1985)
	<i>Mya arenaria</i> Westport population	$2.4 \times 10^{-7}$	planktonic	Present study
	Stonington population	$4.2 \times 10^{-8}$		
	<i>Tapes philippinarum</i>	$1.8 \times 10^{-6}$	planktonic	Yap (1977)
	Gastropoda	<i>Thais lamellosa</i>	$1.9 \times 10^{-3}$	nonplanktonic
<i>Conus pennaceus</i>		$7.0 \times 10^{-4}$	nonplanktonic	Perron (1983)
<i>Lacuna pallidula</i>		$2.0 \times 10^{-4}$	nonplanktonic	Smith (1973)
<i>Aplysia juliana</i>		$2.84 \times 10^{-7}$	planktonic	Sarver (1979)
Crustacea	<i>Balanus glandula</i>	$6.0 \times 10^{-5}$	planktonic	Connell (1970)
	Barnacles (3 spp.)	$2.0 \times 10^{-5}$	planktonic	Hines (1979)

<sup>1</sup>Does not include prehatching mortality.

<sup>2</sup>Survival through 30-d planktonic period only.

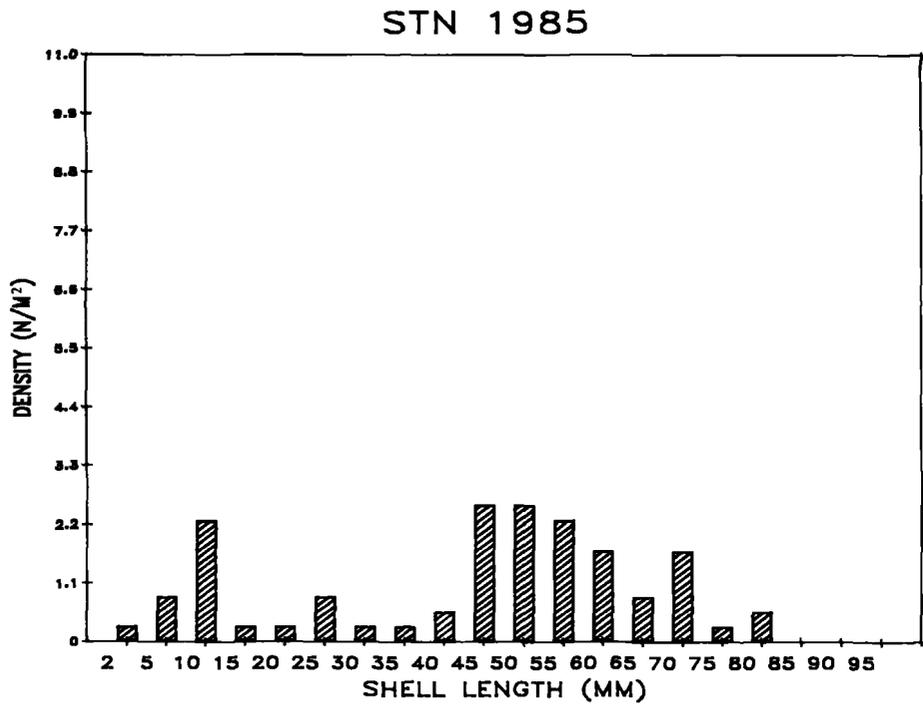
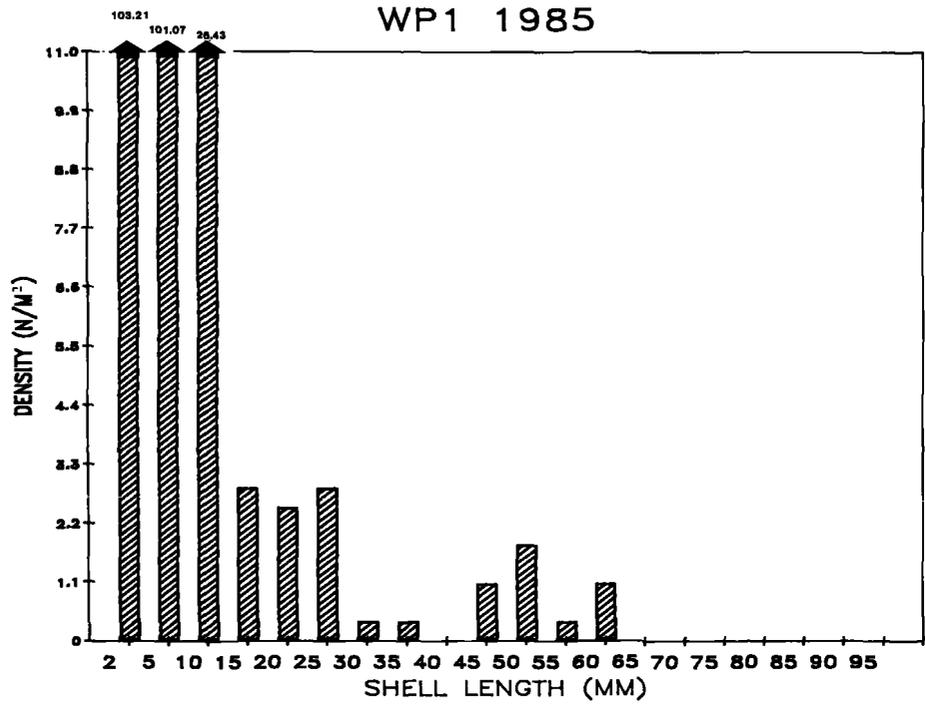
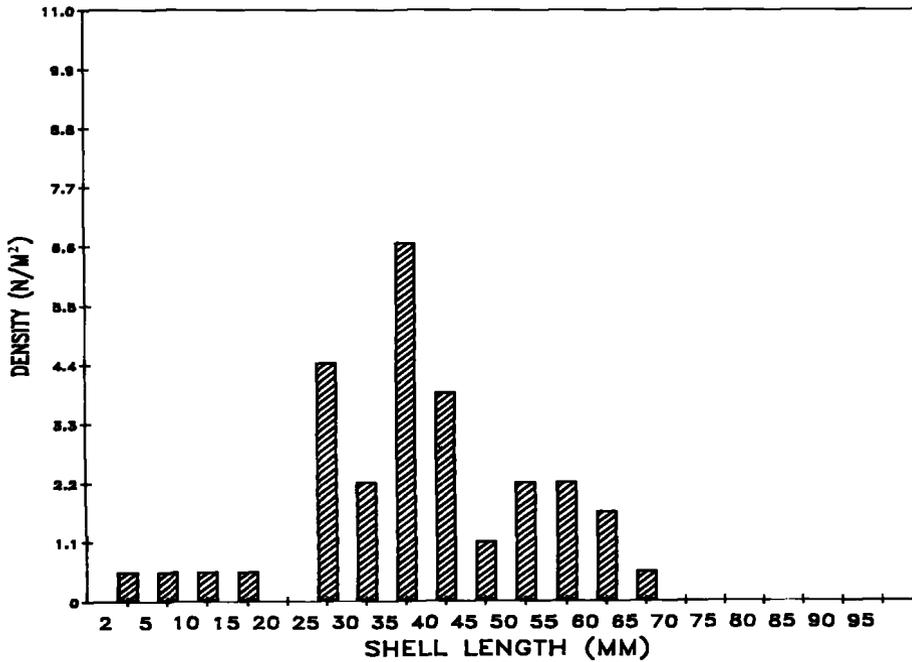


FIGURE 3.—Size-frequency distributions of *Mya arenaria* from the Stonington (STN)

WP1 1986



STN 1986

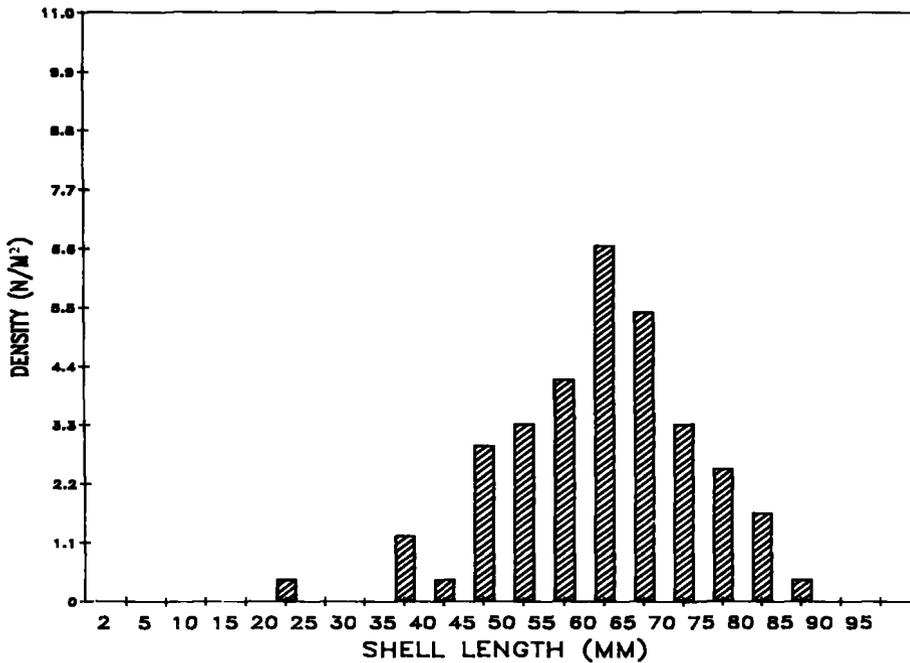


FIGURE 3.—Continued—and Westport (WP1) populations in 1985 and 1986.

The two populations of *M. arenaria* from Long Island Sound appear to show a basic conservatism in general life history pattern. In both populations, fecundity increases rapidly in young females with individuals reaching sexual maturity in time to reproduce at the beginning of their second year of life. Similarly, larval and adult survivorship schedules follow the type III survivorship curve of Deevey (1947). Extremely heavy mortality early in life is followed by roughly constant mortality thereafter. This pattern is similar to that described for a population of *M. arenaria* from Gloucester, MA (Brousseau 1978) except that in the latter, age of first reproduction occurs at the end of the second year. It is interesting to note, however, that some of the major life history features of *M. arenaria* show considerable latitudinal variation within the species. Frequencies of spawnings during the year increases (for review see Ropes and Stickney 1965; Brousseau 1987a) and length of life and body size show a tendency to decrease with decreasing latitude (Belding 1930; Newcombe 1935). Details of the ways in which such variations affect the life history parameters, however, remain to be studied.

The possibility of gene flow between populations of animals with planktonic larval stages always exists. Nevertheless, the amount of genetic overlap is effectively reduced as the geographical distance between the populations increases. The significant quantitative differences in the age-specific demographic parameters for the two populations studied here suggest that within the framework of a general life history strategy, a response to the biotic and abiotic components of the immediate environment is possible. Evidence from this study indicates that environmental conditions at the Westport site may be less optimal for the growth and maintenance of *M. arenaria* than are those at the Stonington site. The higher equilibrium settlement rate calculated for the Westport population indicates that on average, a larger annual spatfall is needed to maintain that population than is required at the Stonington site.

The biotic factors most often cited as agents capable of altering the survival and fecundity of individuals are predation, competition, disease, and parasitism. It is unlikely that predation was a major source of adult mortality at either site for reasons previously discussed. Moreover, the effects of predation would be limited to the small, surface-dwelling clams, since 1) crabs, fish, and birds are unable to capture deep burrowing adults and 2) it has been demonstrated that *M. arenaria* exhibits a "size refuge" from naticid predators (Edwards and Hueb-

ner 1977). Hancock (1973) has suggested that competition for food or space between the spat and adults may contribute to lowered survival in newly settled clams. If this were the case, one would expect lower juvenile survivorship rates in the Stonington population where population densities were greater (Fig. 3).

Trematode infestations have been demonstrated to cause castration and high mortalities in a population of venerid clams, *Transenella tantilla*, in California (Obrebski 1968). Although both trematode infections (Stunkard 1938; Uzman 1951) and fungal parasites have been reported in *M. arenaria* (Andrews 1954), no evidence of either was observed in the 2,826 histologically prepared clams (1,583 from Stonington; 1,243 from Westport) examined in a study of the reproductive cycle in the two populations (Brousseau 1987a). Sarcomatous neoplasia, a proliferative disorder characterized by increased number of "leukemia-like" cells in the tissues and organs (Farley 1969; Brown et al. 1977; Cooper et al. 1982), has been identified in samples of clams from both Stonington and Westport. Prevalence of the disorder in the Stonington population ranges from 0 to 46%, whereas 0–69% of the *M. arenaria* from Westport were neoplastic, depending on the collection date (Brousseau 1987b). At present it is not known if neoplasia is a source of mortality in field populations of clams. It seems reasonable to assume that it is, however, since neoplastic cells are invasive and at times cause the destruction of organs and tissues in infected animals (Yevich and Barszcz 1977). If sarcomatous neoplasms prove to be malignant, this disease could be responsible to some degree for the higher mortality rates reported in the Westport population.

The abiotic factors with the greatest effect on the biotic potential of estuarine organisms are temperature, salinity, substrate, and food availability. Adult *M. arenaria* typically inhabit the intertidal zone and are adapted to a wide range of fluctuations in water temperature and salinity. In addition, sediments tend to buffer temperature and salinity fluctuations (Sanders et al. 1965; Johnson 1965, 1967). Therefore, infaunal organisms like the soft-shell clam are subject to less extreme environmental fluctuations than are exposed organisms living on or attached to the surface. Belding (1930) noted that *M. arenaria* withstands extreme variation in salinity, being able to adjust to changing tides every six hours. Shaw and Hamons (1974) found that lethal conditions for burrowed clams were met only when temperatures persisted in the high 20°C range and salinities were 2‰ or lower. In the laboratory,

adult survival is not altered by salinities of 2.5‰ (Chanley 1957; Pfitzenmeyer and Drobeck 1963; Castagna and Chanley 1973) to 35‰ (Castagna and Chanley 1973). Annual water temperature and salinity patterns in Long Island Sound fall well within the range of conditions tolerated by *M. arenaria* (see Materials and Methods). If temperature and salinity differences did occur, their effects would be minimal.

Substrate differences at the Stonington and Westport sites appear to be the most immediate cause of the observed differences in age-specific fecundity and survivorship. Several investigators have found that sediment type is important in controlling growth rate and shell allometry in *M. arenaria* (Belding 1930; Swan 1952; Newell and Hidu 1982). Clams grown on coarse sediments (gravel, cobble), such as that at the Westport site are slow-growing and more globose in shape than clams from sand or mud environments. Although differences in growth rate could be due to differences in food availability at the two sites, the allometric variations (Brousseau and Baglivo 1987) strongly support the hypothesis that substrate effect is the factor controlling growth. Reduced body size in Westport clams may have an indirect effect on fecundity by restricting egg production. In addition, both Glude (1954) and Pfitzenmeyer and Drobeck (1967) demonstrated that *M. arenaria* burrows fastest in fine-grained sediments since physical resistance to burrowing increases with increasing particle size (Trueman 1954). Hence, the high daily maintenance requirements of Westport clams may result in less energy available for reproduction, long-term maintenance, and survival. The Westport population may be an example of a population inhabiting a marginal environment.

The underlying pattern of life history (reproductive effort, patterns of recruitment, survival profile, and growth schedule) for both populations of *M. arenaria* is very similar. This is not surprising since population parameters are viewed as evolved, species-specific traits. Nevertheless, our evidence for local differentiation in different habitats demonstrates the degree to which individual populations of a widespread species can respond in different ways to their immediate environments; environmental heterogeneity can be reflected in the structures and dynamics of local populations.

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## APPENDIX

APPENDIX TABLE 1.—Empirical distributions for age-size relationships for the Westport, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)								
	1	2	3	4	5	6	7	8	9+
10-20	1 (3.8)								
20-30	9 (34.6)	3 (2.0)							
30-40	13 (50.0)	55 (37.2)	19 (12.7)	2 (2.9)					
40-50	3 (11.5)	70 (47.3)	65 (43.3)	15 (21.4)	7 (15.6)	4 (8.7)	3 (8.3)	3 (7.9)	
50-60		19 (12.8)	60 (40.0)	40 (57.1)	24 (53.3)	23 (50.0)	16 (44.4)	17 (44.7)	6 (23.1)
60-70		1 (0.7)	5 (3.3)	12 (17.1)	13 (28.9)	17 (37.0)	14 (38.9)	14 (36.8)	14 (53.8)
70-80				1 (1.4)	1 (2.2)	2 (4.3)	2 (5.6)	4 (10.5)	6 (23.1)
80-90							1 (2.8)		

APPENDIX TABLE 2.—Empirical distributions for age-size relationships in the Stonington, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)					
	1	2	3	4	5	6+
20-30	15 (26.8)					
30-40	22 (39.3)	4 (5.1)				
40-50	13 (23.2)	5 (6.4)	2 (1.1)			
50-60	6 (10.7)	31 (39.7)	37 (20.2)	5 (3.8)		1 (7.1)
60-70		31 (39.7)	94 (51.4)	26 (19.8)	2 (7.1)	1 (7.1)
70-80		7 (9.0)	41 (22.4)	66 (50.4)	14 (50.0)	4 (28.6)
80-90			9 (4.9)	31 (23.7)	11 (39.3)	6 (42.9)
90-100				3 (2.3)	1 (3.6)	2 (14.3)

