

SPAWNING CYCLE, FECUNDITY, AND RECRUITMENT IN A POPULATION OF SOFT-SHELL CLAM, *MYA ARENARIA*, FROM CAPE ANN, MASSACHUSETTS

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ABSTRACT

A population of *Mya arenaria* in the Annisquam River system, Gloucester, Mass., was studied for 3 yr to determine spawning frequency, fecundity, and recruitment rates under natural conditions. This population was observed to spawn twice each year, in March-April and June-July. Temperature appeared to be a more critical factor in the timing of gonad maturation than in triggering the release of gametes. Female body sizes and oocyte production were positively correlated (1973, $r = 0.95$; 1974, $r = 0.90$). Regression lines were compared by analysis of covariance. Slopes of the lines did not differ significantly between years or between spawning cycles within years ($P \geq 0.05$). Elevations of the lines differed significantly from one another ($P \leq 0.05$) indicating annual and seasonal variability in fecundity. Sex ratios of *M. arenaria* 25-95 mm shell length did not differ significantly from 1:1 over the 3-yr study period. In smaller individuals, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry was observed. Recruitment rates of juveniles fluctuated widely between spawning cycles as well as between years.

Although the literature contains widely scattered references to the reproductive cycle of *Mya arenaria* in New England, there is no combined account of egg production (= fecundity), spawning, and recruitment of this species under natural conditions. Inferences about the time and frequency of spawning by *M. arenaria* have been made from observations on larvae in the plankton (Stevenson 1907; Stafford 1912; Sullivan 1948; Landers 1954; Pfitzenmeyer 1962); from first appearances of newly settled juveniles (Belding 1930; Warwick and Price 1975); and from the presence of ripe gametes in the gonads (Battle 1932; Coe and Turner 1938; Shaw 1962; Stickney 1963; Ropes and Stickney 1965; Munch-Peterson 1973; Porter 1974). Observations on larvae and recently metamorphosed clams, however, are useful only as indirect measures of the frequency and duration of spawning, since larval abundance and juvenile recruitment are controlled by factors other than spawning alone. Conversely, evidence concerning gonad maturation and gamete release obtained by means of histological methods defines the spawning period without contributing to knowledge about recruitment.

Most shallow-water marine animals reproduce in a cyclic manner, the time of spawning ultimately depending on environmental factors (Orton 1920; Giese 1959; Kinne 1963). As with most other commonly studied bivalves, the timing of spawning by *M. arenaria* has been linked to water temperatures (Nelson 1928; Belding 1930; Battle 1932). Nevertheless, it remains unclear whether gametogenesis, spawning, or both occur at a specific temperature or in a specific temperature range in *M. arenaria*.

Reliable information on fecundity of *M. arenaria* is also unavailable. Laboratory methods for stripping eggs or inducing spawning in oysters and hard-shell clams (Brooks 1880; Churchill 1920; Galtsoff 1930; Belding 1930; Davis and Chanley 1956; Loosanoff and Davis 1963) are generally unsuccessful with *M. arenaria*. Consequently, the only information on egg production by *M. arenaria* is an unsupported statement by Belding (1930) that a 2.5-in clam (63 mm) produces about 3 million eggs per breeding season.

In an effort to clarify the breeding habits of *M. arenaria*, this study was designed to determine 1) the reproductive cycle in a natural population, 2) the temperature at which gametogenesis and spawning begin in this locale, and 3) the total numbers of eggs produced by individuals of different sizes.

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MATERIALS AND METHODS

The Annisquam River is a natural waterway approximately 3 mi long connecting Ipswich Bay on the north side of Cape Ann peninsula with Gloucester Harbor on the south (Figure 1). The

river consists of a dredged channel with extensive tidal mud flats or shallow water on both sides. The mean tidal amplitude at Gloucester Harbor is 3 m. The Annisquam River receives limited freshwater drainage, resulting in salinities of 28-33.5‰. Water movement is largely dependent on the tides. Average monthly surface water temperatures (1 m depth) for the years 1973 and 1974 obtained from the University of Massachusetts Marine Station at Hodgkins Cove (Figure 1) indicate that monthly temperature fluctuations are great (Figure 2). Temperature data for 1975 were not available.

The site for this study was located on a mudflat along the west bank of the Jones River, a small tributary opening at the northern end of the Annisquam River (Figure 1). Historically, this area has been the site of a productive shellfish bed and is known to sustain numerous clams of differing age classes (Mass. Dep. Resour., Div. Mar. Fish. pers. commun.).

The study began in February 1973 and was completed in October 1975. Clams were collected from the middle of the intertidal zone (+1 m tidal level) once a month from October 1973 through February 1974 and October 1974 through October 1975, and twice a month from March through September 1973 and April through August 1974. No samples were taken in September 1974 or in May, June, July, and September 1975. Sample sizes varied greatly. Samples collected during the spring and summer months consisted of 30 to 127 clams, 21-90 mm shell length. Those collected during the winter months consisted of 15 to 30 clams each in a similar size range. Large numbers of clams were

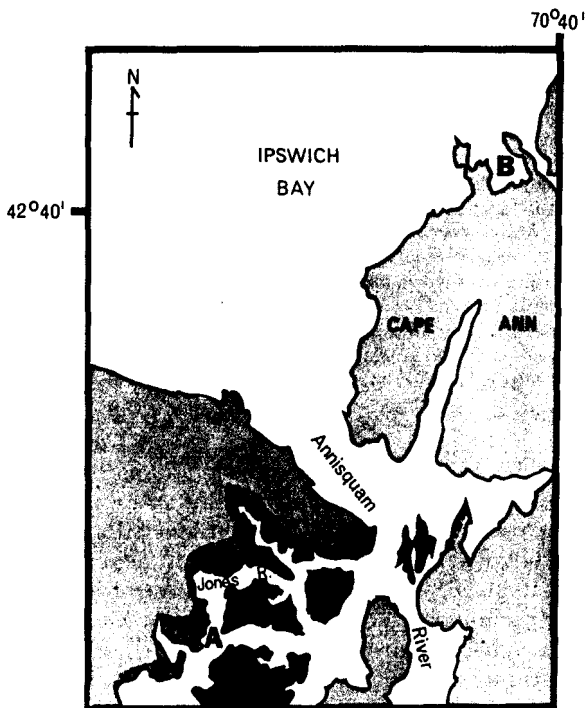


FIGURE 1.—Map showing locations of the Jones River study site (A) and the University of Massachusetts Marine Station, Hodgkins Cove (B).

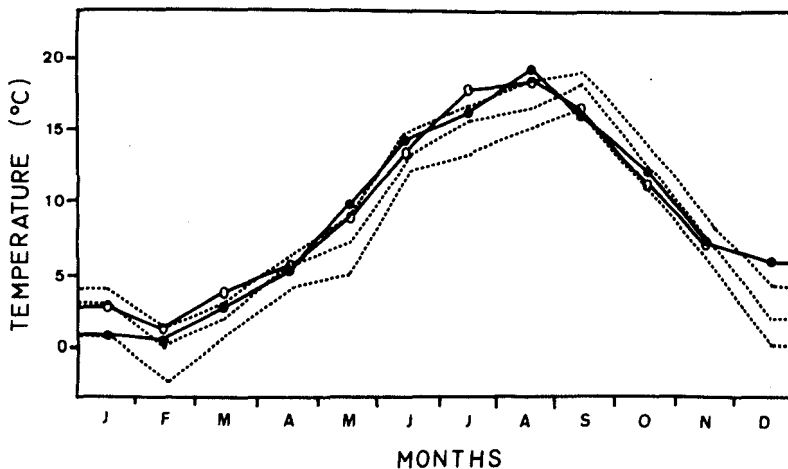


FIGURE 2.—Sea-surface (1 m depth) temperatures for Hodgkins Cove, Gloucester, Mass. Monthly means for 1973 (●●) and 1974 (○○) are plotted. The dashed lines represent 8-yr average maxima, means, and minima for the period 1963-71, based on temperatures for the Portland Lightship (Chase 1965-1973) corrected for Hodgkins Cove.

collected during the spawning season in order to insure sufficient numbers of "ripe" females for fecundity studies. A total of 2,480 clams were examined of which 11% were immature, leaving 2,206 mature clams that were used in the analysis of the reproductive cycle.

The samples were returned to the laboratory where they were kept at 0°C for not more than 3 days before being dissected. Each clam was numbered and its maximum length (± 0.1 mm) determined. The visceral mass (gonad, liver, and gastrointestinal tract) was taken out and fixed in 10% buffered Formalin² (Humason 1967). The displacement volume of each visceral mass was taken to determine its size. The amount of gonadal tissue present was determined after sectioning by the planimetry method described below. The fixed mass was then dehydrated in alcohol, embedded in paraffin, sectioned at 8 μ m, and stained in Harris' hematoxylin and eosin. Each clam was classified with respect to gonad development and the number in each developmental stage was recorded for both sexes.

Previous studies on the gonadal cycles of *Mya arenaria* have divided the developmental sequence into five morphologically distinct phases: inactive, active ripe, spawning, and spent (Ropes and Stickney 1965; Porter 1974). Since semantic problems arise with this usage, several terms are redefined for use here. The term "indifferent" is preferred to "inactive" to describe low levels of oogenic and spermiogenic activity. As pointed out by Keck et al. (1975) in work on hard clam gonadal cycles, the term "inactive" is biologically inaccurate since it implies a "static condition where absolutely no morphological or biochemical activity is proceeding." The term "developing" is used when describing the onset of gametogenesis since it can be argued that ripe and partially spawned gonads are active in the sense that gametogenic activity continues at a reduced level. Developing, ripe, and partially spawned stages are collectively termed "active," whereas spent and indifferent stages are termed "inactive." This distinction aids in defining peaks of spawning within the annual cycle.

Recognition of the five phases of gonadal condition was based on the same characteristics as those used by other investigators (Ropes and Stickney 1965; Porter 1974).

The number of oocytes present in each female gonad was determined in the following manner. Using an ocular grid, triplicate counts were made of the number of oocytes present per 0.49 mm² of gonad for each female reported in a ripe condition. This area was then multiplied by the mean oocyte diameter (0.65 mm) in order to determine oocyte densities on a cubic basis. An estimate of the total number of oocytes in the gonad could then be calculated on the basis of gonad size. Analysis of variance confirmed that the number of oocytes per unit volume was constant throughout the ripened gonad ($P \leq 0.05$).

Mean oocyte diameter was determined for a representative sample of ripe females, selected at random from each of the reported spawning periods. Twenty oocytes per clam were measured using an ocular micrometer. Only those oocytes which were spherical in shape and ready for release were selected for measurement.

The relationship between the size of the ripe female gonads and the volume of the total visceral mass was determined as follows. Entire viscera from 17 ripe females (53-76 mm shell length) were sectioned at 12 μ m. Next, 18 sections from each individual were chosen at random, mounted on a Plexiglas base and fitted into a 35-mm slide projector and the projected tissue outlines were traced. A planimeter was used to estimate the percentage of gonad tissue present. A correction factor representing the proportion of gonad in the total visceral mass was used in estimating the total number of oocytes per individual (0.763 ± 0.21 , 95% C.I.).

Photographs of representative stages of the female reproductive cycle were taken with a light microscope at 160 \times and 100 \times magnification using a 35-mm camera. High contrast, Panatomic X ASA32 film was used.

Densities of juvenile *M. arenaria* were tabulated from the monthly samplings of the tidal flat during October 1973, from May to November 1974, and in November 1975. At each sampling period, 12 random samples (0.11 m², 20 cm deep) were taken along a 90-m transect from mean low water shoreward to the marsh scarp. Samples were wet sieved in the field (2-mm mesh) and the size-frequency distribution of the clams was determined. Cohorts in the population were isolated by the probability paper method (Harding 1949; Cassie 1954).

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Reproductive Cycle

Reproductively active individuals were encountered throughout the 3-yr study period, the largest numbers occurred in April and July of 1973, March and early July of 1974, and mid-March of 1975 (Figure 3). Due to the limited sampling undertaken during the summer of 1975, the summer spawning peak cannot be determined with certainty.

In February 1974, gametogenesis had begun in both sexes (Figure 4). Ripe and partially spawned clams were observed in mid-March. By late April,

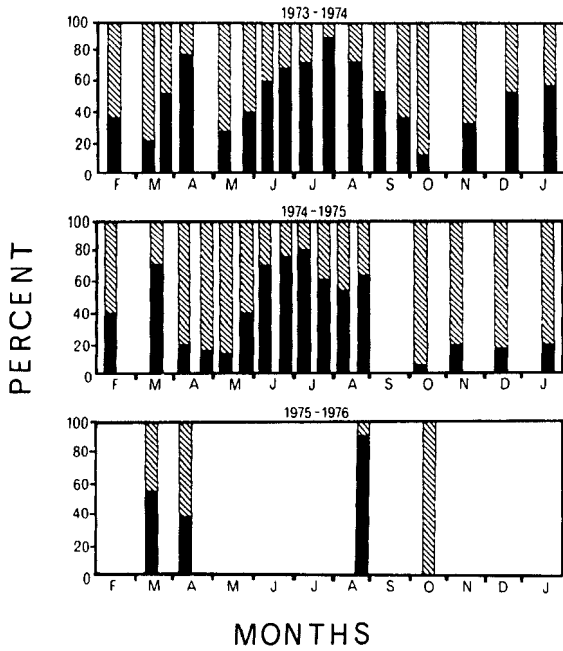


FIGURE 3.—Proportions of *Mya arenaria* population with active or inactive gonads during 1973-74, 1974-75, and 1975-76. Cross-hatched portions of each bar represent inactive gonads (indifferent, no gametogenesis, or spent); solid portions represent active gonads (developing, ripe gametes, or partially spent). Observations on males and females were combined.

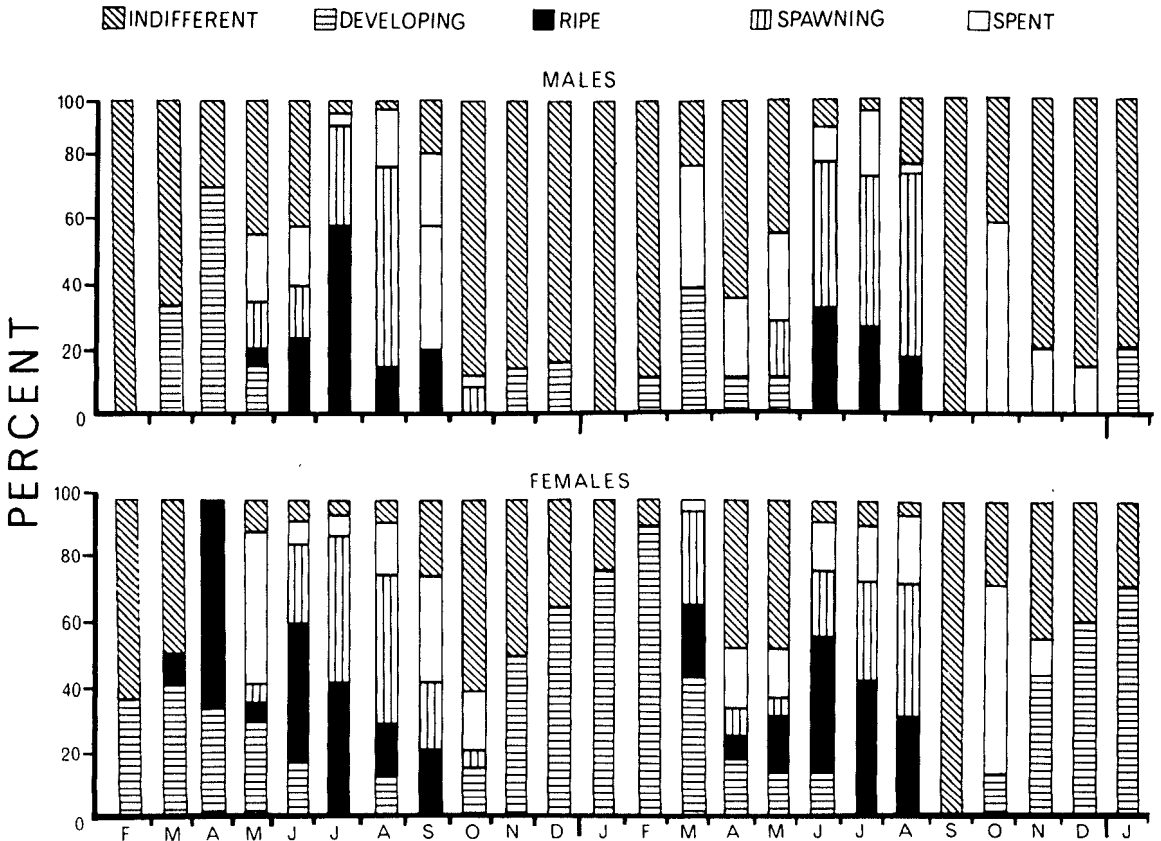


FIGURE 4.—Proportions of male and female *Mya arenaria* with gonads in each developmental phase during 1973-74 and 1974-75.

about 75% had completely spawned and returned to the indifferent condition. Gametogenesis usually resumed after spawning, and by early June about one-quarter of the clams were again ripe and partially spawned. The presence of cytolyzed unspawned gametes in the summer samples suggested that the same individuals had also been ripe earlier in the year. Thus the observed spawning pattern was due to repeated spawning by the same individuals rather than asynchronous spawning of individuals within the population.

A similar spawning pattern was observed in 1973, except that gametogenesis did not begin until April (Figure 4) and the summer spawning peak occurred in July rather than late June-early July. The data for both years indicate a more or less consistent recovery period between reproductive cycles. The data for the 1975 season indicate that spring spawning occurred in March as it did in 1974, but the summer sampling intervals were too irregular to describe details of the summer spawning. Nevertheless, occurrence of a summer spawning is confirmed by the gonad condition of the clams in the August sample.

Photomicrographs of representative female stages in the spring and summer peaks of the annual cycle are shown in Figure 5. The pattern of development in the clams during the spring cycle differs from that of the later summer one. In the female, the spring cycle is characterized by rapid gametogenesis, resulting in smaller oocyte size and fewer numbers of oocytes produced per unit of gonad tissue (Table 1), so different density values were used for calculations of fecundity (gonad volume \times density) in different seasons. A significant seasonal difference in the diameter of ripe oocytes of female *M. arenaria* was detected using one-way analysis of variance ($P \leq 0.05$). Similarly, male clams appear to undergo rapid maturation and produce fewer gametes than during the summer spawning. Fully ripe males were not encountered in any of the spring samples, however, spent males were numerous, indicating that spawning had taken place. Spring spawning may be a facultative event, characterized by rapid maturation and the subsequent utilization of the abundant food supply that is available during the major phytoplankton "bloom" that occurs nearshore during this period.

Temperature is an important factor influencing the gonadal cycle in a variety of marine bivalves (Loosanoff 1937a, b; Landers 1954; Giese 1959; Carriker 1961; Ansell et al. 1964; Galtsoff 1964;

Calabrese 1970). If temperature is indeed a factor in the onset of reproduction in *M. arenaria* as previously believed (Nelson 1928; Belding 1930), short-term temperature patterns in winter and early spring should correlate with the annual timing of gametogenesis (Figure 4). In fact, temperatures during January-March 1974 averaged about 2° higher than during the same period of the previous year (Figure 2) and gametogenesis began a month earlier than in 1973.

The actual role of temperature in the timing of gamete release remains unclear. Spring spawning peaks occurred at surface water temperatures of 4°-6°C and summer spawnings at 15°-18°C. Although the interstitial water of exposed tidal flats warms up considerably during midday spring lows (Johnson 1965), it is unlikely that interstitial temperatures would be high enough to account for these differences. If these is a critical minimum temperature for spawning it is at or above 4°-6°C. No maximum limit can be discerned from these data. The role of rapid temperature change in triggering spawning as suggested by other authors (Battle 1932; Stickney 1963) has not been assessed here.

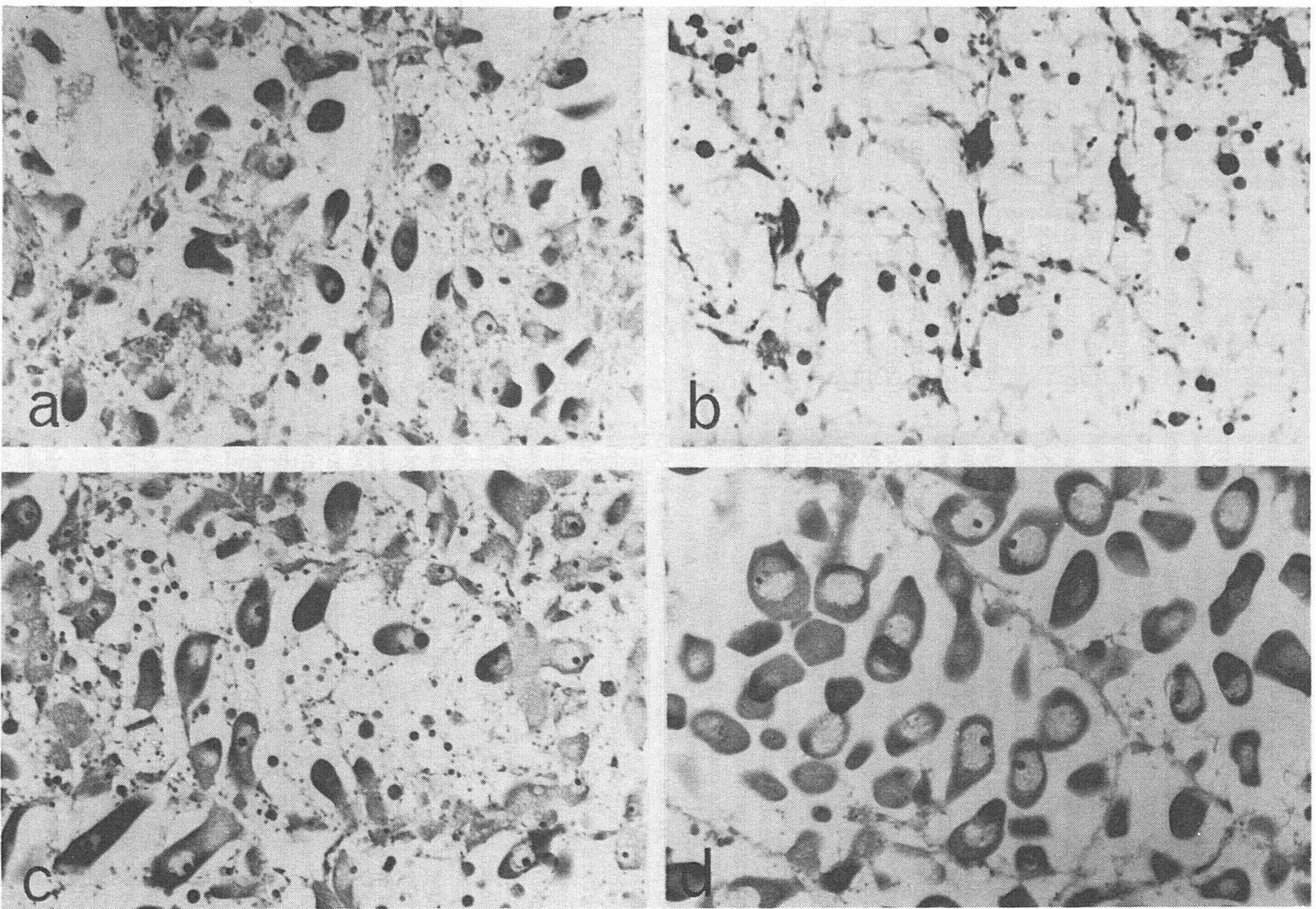
Sex Ratios and Fecundity

The reproductive potential of a population depends, in large part, on the number of fertile females and the number of young produced per female. The proportion of females in all size-classes in three large samples from the Jones River in 1973 ($n = 1,266$), 1974 ($n = 859$), and 1975 ($n = 150$) did not differ significantly from one-half. In size-classes <25 mm, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry was observed.

The number oocytes produced was found to increase exponentially with increasing female body size. The regression equations for oocyte numbers (O) versus female shell length (S) are:

$$\begin{aligned} \text{Spring 1973: } \log_{10} O &= -1.45 + 3.29 \log_{10} S \\ \text{Summer 1973: } \log_{10} O &= -1.29 + 3.28 \log_{10} S \\ \text{Spring 1974: } \log_{10} O &= -0.90 + 2.91 \log_{10} S \\ \text{Summer 1974: } \log_{10} O &= -1.42 + 3.32 \log_{10} S \end{aligned}$$

Comparison of the regression lines by analysis of covariance indicated that the lines were parallel ($P \geq 0.05$) but the elevations of the lines were significantly different ($P \leq 0.05$). Total oocyte production during 1973 was greater than during 1974.



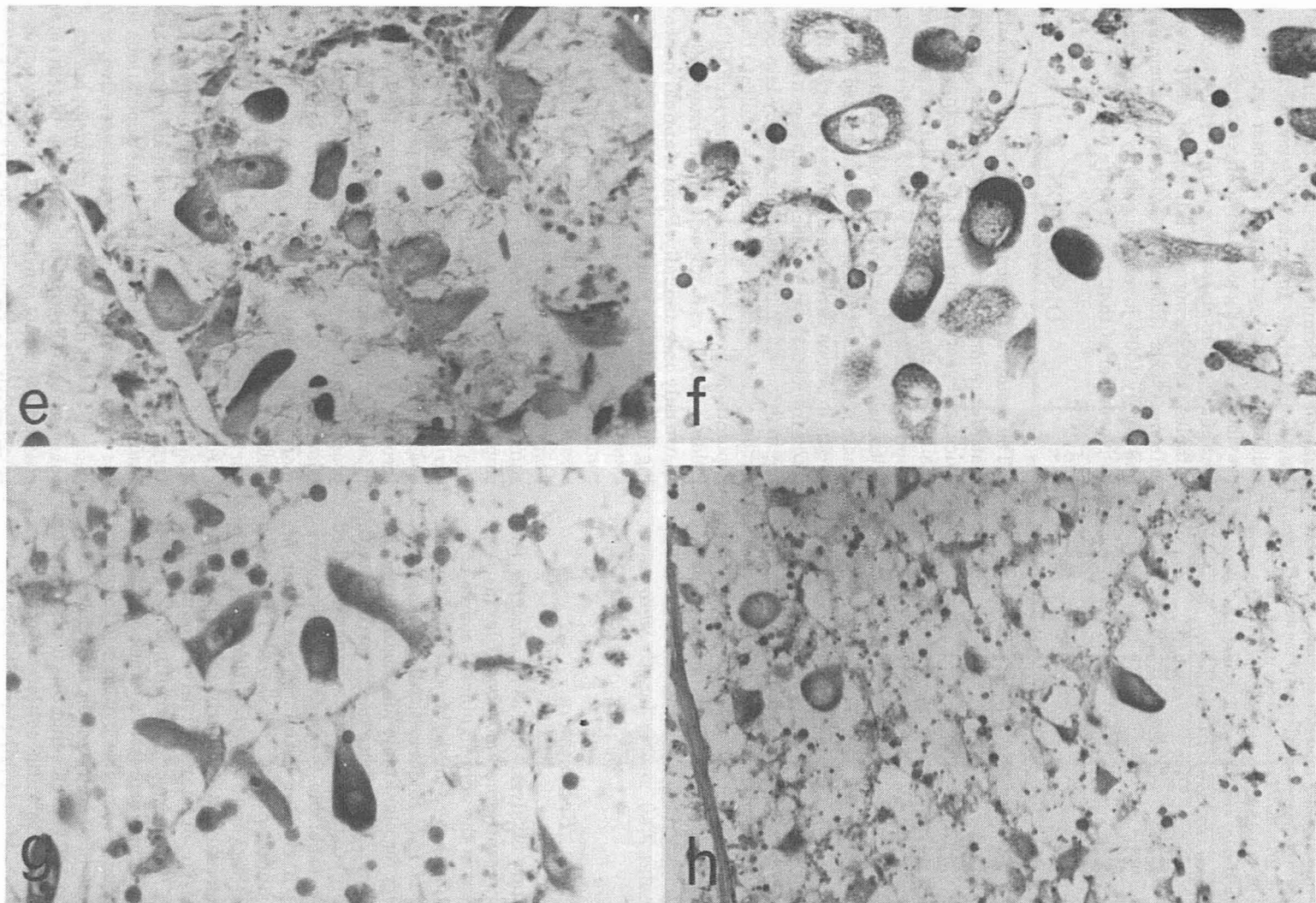


FIGURE 5.—Photomicrographs of gonadal stages of the soft-shell clam, *Mya arenaria*. a) Developing female (100X), 7 April 1973; b) Developing female (100X), 21 May 1973; c) Ripe female (100X), 24 March 1973; d) Ripe female (100X), 1 July 1973; e) Partially spawned female (160X), 16 March 1974; f) Partially spawned female (160X), 1 July 1973; g) Spent female (160X), 5 May 1973; and h) Spent female (100X), 1 July 1973.

TABLE 1.—Oocyte diameter (microns) of "ripe" female *Mya arenaria* from each of the spawning periods of the annual reproductive cycles of 1973-75. Values represent the means of measurements on 20 individual oocytes per clam. The number of individuals sampled (n) and the overall means (\bar{x}) are given.

Spring 1973	Summer 1973	Spring 1974	Summer 1974	Spring 1975
48.3	57.9	41.0	59.0	39.3
42.4	66.9	40.4	58.0	45.2
43.1	62.8	40.7	56.9	41.0
44.5	62.4	40.0	73.8	44.2
43.5	43.5	41.0	60.4	39.9
41.4	61.1	42.1	63.1	43.8
43.8	61.8	33.3	68.0	42.4
45.2	64.2	40.4	63.1	41.0
51.4	64.5		58.6	36.2
	64.9		59.7	42.1
	61.8		58.6	36.2
	64.9		55.2	40.7
	63.1		68.0	37.3
	62.8		65.2	41.0
	61.1		61.1	40.4
	63.1		62.8	46.2
	62.8		58.3	
	64.2		64.9	
	61.1		64.9	
	50.0		65.9	
	52.8		71.1	
	58.3		71.8	
	58.0			
n	9	8	22	16
\bar{x}	44.7	60.6	63.1	41.2

The limited data available for 1975 were not analyzed. In addition, fecundity differed between spawning seasons within a single year. Oocyte production was larger during the summer spawning cycle than during the spring one in 1973 and 1974. Females <40 mm in length were never gravid.

Recruitment

In sedentary bivalves, such as *M. arenaria*, settlement of recently metamorphosed larvae from the plankton is the only significant source of recruitment. Spat were most abundant in May and September of 1974 (Figure 6). Allowing approximately 5 wk for planktonic life, metamorphosis, and growth to 2 mm, these peaks correlate with and probably result from the spawnings described above. This timetable for metamorphosis corresponds with similar estimates made for *M. arenaria* under natural (Kellogg 1905) and laboratory (Stickney 1964) conditions.

Large fluctuations in yearly recruitment are characteristic of many bivalve populations (Hughes 1970). Therefore, recruitment of young, when it occurs, may represent a large proportion of the population. A comparison of the size-frequency distributions in samples taken in October 1973 and October 1974 reveals that this is also true for *M. arenaria*. A substantial settlement occurred in May of 1974, but by the fall, this cohort had nearly

disappeared. Similarly, the fall set (Figure 6, 1B) quickly vanished. In contrast, survival of individuals from the spring and summer sets in the previous year was good, as evidenced by the numbers of these size-classes persisting in the October samples. The spring and fall sets of 1975 were extremely poor (Robert Knowles pers. commun.) and nearly 100% juvenile mortality had occurred by November of that year (Figure 6).

DISCUSSION

The results of the gonad examinations indicate that *M. arenaria* from Gloucester, Mass., spawn twice each year (Figure 3). This spawning pattern is similar to that reported for populations south of Cape Cod (Mead and Barnes 1903; Landers 1954; Pfitzenmeyer 1962), although isolated instances of single spawnings have been documented (Shaw 1962). Previous investigators have reported that clams from northern Massachusetts began spawning in July and completed spawning by late September. There is strong evidence to indicate that populations from Plum Island Sound studied by Belding (1930) and Ropes and Stickney (1965), spawn only once annually. Proof of annual spawning in populations south of Plum Island Sound to Cape Cod, however, is less convincing. Based on the presence of larval *M. arenaria* in plankton samples, Stevenson (1907) reported that clams from Ipswich and Plymouth spawn in the late summer. It is not clear from his report whether sampling was conducted year-round or only during the summer months. If the latter is true, then early spring spawning activity may have been overlooked and the later summer peak (Figure 3) incorrectly interpreted as evidence for a single late spawning season for clams of this area. It is possible that the biannual spawning observed in Gloucester is a local phenomenon. Nevertheless, more work is needed before any generalizations concerning the frequency of spawning of clams in northern Massachusetts can be made.

Indirect evidence also gives clear indication of a biannual spawning cycle. First, recruitment patterns both corroborated the evidence from gonad examinations and indicated other populations in the area spawned at the same times. Owing to pelagic larval dispersal in *M. arenaria*, bursts of recruitment (Figure 6) would be obscured if spawning were not synchronous in nearby populations. Secondly, sea-surface temperatures for 1973

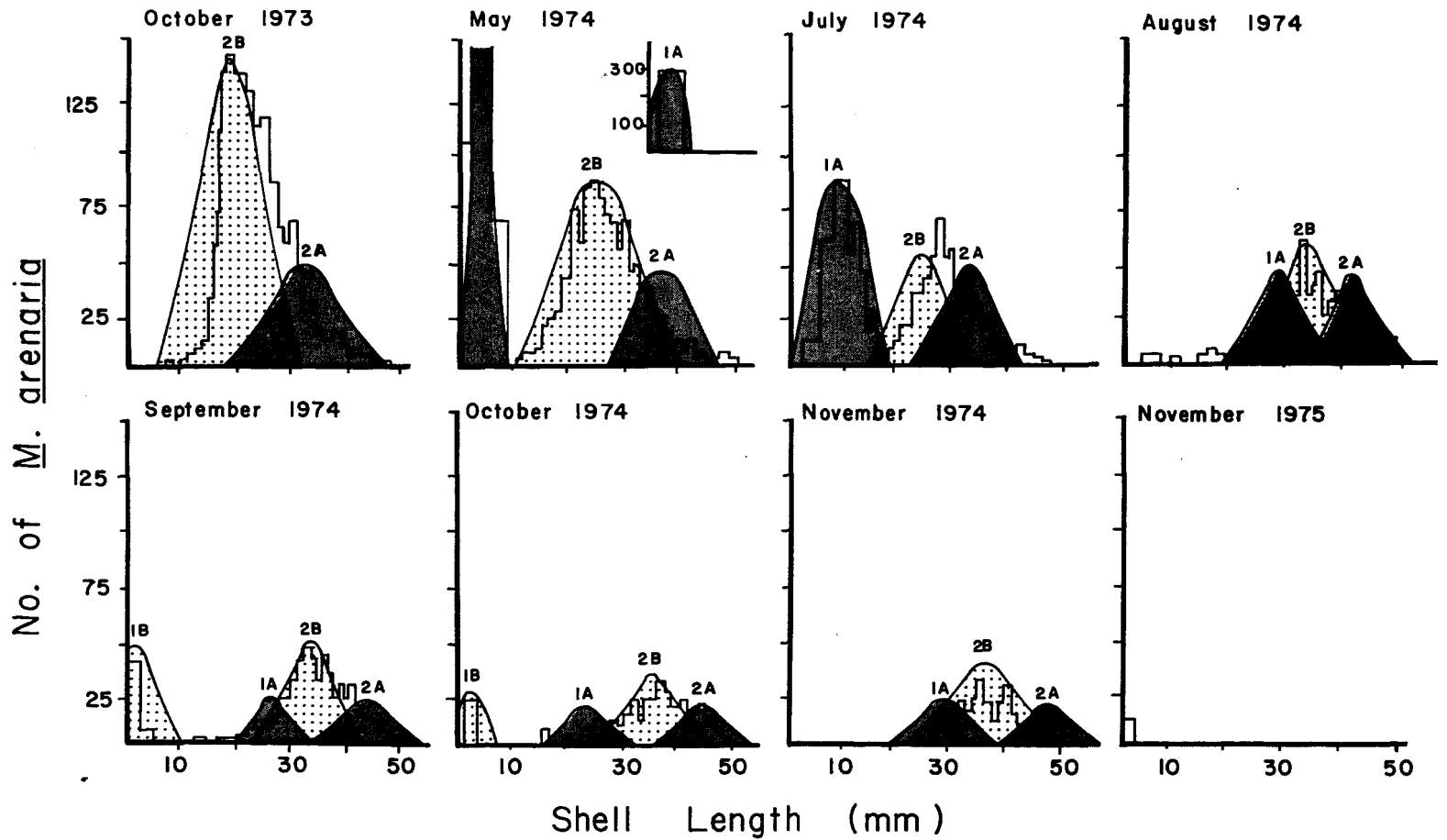


FIGURE 6.—Size-frequency distributions of *Mya arenaria* during October 1973, May–November 1974, and November 1975. Normal curves obtained by probability paper analysis are indicated by shading. Numerals indicate the year class of each cohort (0 = 1975; 1 = 1974; 2 = 1973) and letters denote the season in which the set occurred (A = spring; B = summer).

and 1974 approximated 8-yr monthly means so the bimodal pattern was not an atypical response to above average temperatures. Nevertheless, the temperature patterns of this locale are probably influenced substantially by local topography. More than 60% of the total area of the Annisquam River system is <6 m deep, 30% being intertidal (Jerome et al. 1968). Early spring warming and fall cooling trends would be expected here due to these nearshore influences. Lastly, it appears that the bimodal spawning pattern emerging here may be typical of some populations of *M. arenaria* found as far north as Plum Island Sound. A spring set of juvenile clams occurs annually on intertidal flats in Ipswich, Mass., (Richard Sheppard pers. commun.) and large numbers of 2- to 4-mm clams appeared in the May and June samples of Smith et al. (1955). Such evidence indicates that a semian- nual pattern may be more prevalent in northern Massachusetts than once believed.

Orton (1920) first noted that some animals in temperate regions spawn when the temperature exceeds a critical level characteristic of the species, while for others the rate of change is important. Nelson (1928) reported 10°-12°C as the critical spawning temperature for *M. arenaria*; Belding (1930) reported the exceptionally high figure of 22°C. The data for Gloucester indicate that spawning can occur with equal likelihood at either of the supposedly critical temperatures provided that the gonad is ripe. The significant temperature appears to be that at which maturation of the gonad occurs. Similar significance of maturation temperature had been reported for the oyster, *Crassostrea virginica*, by Loosanoff and Davis (1950).

Gonadal oocyte counts provide an accurate measure of fecundity in *M. arenaria* since all oocytes are stored in the gonad prior to spawning and nearly total evacuation takes place at spawning. The fecundity values for *M. arenaria* indicate that the largest females produce the largest number of oocytes. This increase is undoubtedly due to increased gonad size made possible by increased shell volume. Average oocyte production by a 60-mm clam during a single breeding season (two spawning periods) is about 120,000; lifetime production would be in the order of 1.5×10^6 oocytes. Although fecundity of *M. arenaria* is large, as is typical of species with planktonic larvae (Thorson 1950), these estimates are considerably lower than early unsubstantiated ones for this species (Belding 1930), as well as those reported for other

marine bivalves such as *Crassostrea virginica* and the hard-shell clam, *Mercenaria mercenaria* (Galtsoff 1930; Davis and Chanley 1956).

High fecundity, however, is offset by high mortality during pelagic life, metamorphosis, and early settlement. It appears that sources of mortality such as predation, disease, and bottom character are more critical factors in explaining fluctuations in recruitment than variability in fecundity rates or spawning frequency. The spawning cycles in which the greatest number of oocytes were released did not correlate with periods of highest recruitment. In terms of spat densities, spring recruitment in both years studied was higher than summer recruitment. Success of some year classes and failure of others indicate that fluctuations in clam populations are largely natural occurrences and may result from things other than fluctuations in the number of oocytes or the number of juveniles or byssus-stage young.

Spawning times and fecundities of individual females are critical factors in determining first, what constitutes a satisfactory breeding stock and secondly, how to protect it. Numerous studies have been conducted on methods of improving soft-shell clam fisheries (Belding 1930; Turner 1949, 1950; Smith et al. 1955; Smith³). Regulatory efforts have ranged from predator control to establishment of legal size limits for clams, closed seasons, and restocking of barren flats. All this work has proceeded in the near absence of basic information of the reproduction and population dynamics of the clam. The dwindling yields of clams on the New England coasts indicate the ineffectiveness of present regulatory procedures and the need for revised management practices.

In Massachusetts, any clam over 2 in long (51 mm) may be harvested. In effect this practice maximizes the removal of the reproductively most valuable individuals in the population. Murphy (1968), using genetic models, has shown that adult longevity and iteroparity (= repeated reproduction) are important adaptations for population stability in species like *M. arenaria* which exist under conditions of uncertain preadult survival and relatively stable adult survival (Brousseau

³Smith, O. R. 1952. The results of experimental soft clam farming in Plum Island Sound, Massachusetts. Third annual conference on clam research, U.S. Fish and Wildl. Service, clam investigations, Boothbay Harbor, Maine, p. 46-48. Unpubl. rep.

1976). Consequently, long-term stability of the resource is endangered by present harvesting practices which reduce the normal 10-12 yr lifespan of *M. arenaria* to 2 yr. Revision of existing regulations to include protection of sufficient breeding stock may be an effective way of insuring the long-term stability of the resource and minimizing the harmful effects of human predation.

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