LEWIS, R. M., AND C. M. ROITHMAYR.
    1981. Spawning and sexual maturity of gulf menhaden,
        Brevoortia patronus. Fish. Bull., U.S. 78:947-951.
McGURK, W. D.
    1984. Effects of delayed feeding and temperature on the age
        of irreversible starvation and on the rates of growth and
        mortality of Pacific herring larvae. Mar. Biol. 84:13-26.
MURPHY, G. I.
    1968. Pattern in life history and the environment. Am. Nat.
        102:391-403.
NICHOLSON, W. R.
    1975. Age and size composition of the Atlantic menhaden,
        Brevoortia tyrannus, purse seine catch, 1963-71, with a brief
        discussion of the fishery. U.S. Dep. Commer., NOAA Tech.
        Rep. NMFS SSRF-684, 28 p.
    1978. Movements and population structure of Atlantic men-
        haden indicated by tag returns. Estuaries 1:141-150.
REINTJES, J.
    1969. Synopsis of biological data on the Atlantic menhaden,
        Brevoortia tyrannus. U.S. Fish Wildl. Serv., Circ. 320, 30
        p.
STEARNS, S. C.
    1976. Life-history tactics: a review of the ideas. Q. Rev. Biol.
        51:3-47.

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SEASONALITY OF BLUE MUSSEL, *MYTILUS EDULIS* L., LARVAE IN THE DAMARISCOTTA RIVER ESTUARY, MAINE, 1969-77[1]

The spawning of the blue mussel, *Mytilus edulis* L., has been the subject of many studies (see Bayne 1976 for partial review). In an early paper Field (1922) reported that gametogenesis and spawning were influenced by water temperature, though he provided no data. Chipperfield (1953) found that mussels spawn over a specific range of water temperature (9.5°-12.5°C). In addition, Chipperfield noted that the rate of temperature change prior to spawning influences intensity. Other investigators have found that mussels spawn over a specific temperature range, which may vary among locales

(Engle and Loosanoff 1944; Stubbings 1954; Baird 1966; Bohle 1971; Rasmussen 1973; Jorgensen 1981; Kautsky 1982).

Seed (1975) summarized reproduction in European mussel populations and found that spawning in *M. edulis* varies with latitude, occurring earlier in warm waters and progressively later in cooler, northern waters. However, Newell et al. (1982) reported no latitudinal variation of spawning among mussel populations along the northwestern Atlantic coast. Such geographic variation has been attributed to the existence of physiological races (Stauber 1950; Loosanoff and Nomejko 1951). Newell et al. (1982) and Fell and Belsamo (1985) also found that mussel populations at the same latitude in Long Island Sound spawn at different temperatures and times of the year. They surmised that food availability, rather than temperature, dictates when spawning occurs.

Factors which are important in the timing and intensity of spawning can be determined by monitoring spawning activity. This may be achieved directly, by examination of gonad development in seasonally collected samples, or indirectly, by observing the presence or absence of *M. edulis* larvae in plankton samples (Chipperfield 1953). While the direct method is preferable, the indirect method does allow one to use long-term plankton records. These provide an estimate of the variation in both the timing and intensity of spawning. Since the source of the larvae is not certain, some caution should be used in the interpretation of the results (Seed 1975).

An 8-yr plankton record of *Mytilus* larval abundance presents an unusual opportunity to observe long-term variability in spawning and larval occurrence. Specifically, the data were examined with the following goals:

1) Determination of the initiation and the duration of the spawning season and degree of temporal variation between years;
2) Determination of the variation in larval abundances within and between seasons;
3) Examination of the possible correlation of environmental variables (temperature, phytoplankton abundance, degree days, calendar date, and lunar cycles) with spawning activity.

Materials and Methods

The study site was the Damariscotta River estuary (Fig. 1), a narrow embayment, 29 km long, which receives a limited amount of freshwater. The estu-

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arine portion has a MLW (mean low water) volume of 123.4×10^6 m³, a tidal volume of 56.2×10^6 m³, and a mean summer flushing time of 4-5 wk

FIGURE 1.—Location map.

(McAlice 1977). The estuary is stratified near its head but approaches a well-mixed condition further seaward. Tides are semi-diurnal with a mean range of 2.7 m and a tidal excursion of about 2.8 km (Lee and McAlice 1979).

Monthly-plankton samples were collected during daylight at station D7 (Fig. 1) from October 1969 to June 1970 and then biweekly until September 1977. Plankton tows were 10-15 min oblique hauls with #20 mesh (76 μm) nets of 0.5 m mouth diameter equipped with centrally mounted flowmeters. Maximum depths of tows were 10-15 m (4-5 m above the bottom). Boat speed was 1-2 m s⁻¹. Samples were immediately fixed in 4% buffered Formalin[2].

Laboratory subsampling followed the method recommended by Frolander (1968). The concentrated plankton was diluted to a known volume, thoroughly stirred, and a 1 mL aliquot removed with a Stempel pipette. Initial counts on samples taken from June 1974 to September 1977 did not distinguish among taxa of larval bivalves. We therefore took an additional subsample, determined the percentage of *Mytilus* in 50 bivalve larvae, and multiplied this by the total veliger abundance to obtain *Mytilus* densities for each sampling period.

Several key publications (Loosanoff et al. 1966; Chanley and Andrews 1971; DeScweinitz and Lutz 1976; Lutz and Hidu 1979) containing photomicrographs and descriptions were used to identify *Mytilus edulis* larvae. The differentiation of *Mytilus edulis* larvae from other mytilid larvae (*Modiolus modiolus* and *Geukensia demissa*) at the straight hinge stage was achieved by comparing the length of the hinge line as well as total shell length and height. The early and late umbo larvae of *Geukensia* were easily distinguishable by their elongated appearance; *Mytilus* larvae tended to be less elongate, though pointed anteriorly (Chanley and Andrews 1971). The differentiation of *Modiolus modiolus* larvae and *Mytilus edulis* larvae was based mainly on the characteristics described by DeSchweinitz and Lutz (1976); hinge line lengths, total shell length in the 95-105 μm range, shell shape of umbo stage larvae, presence of an eye spot in specimens <270 μm, and the presence of a functional foot in larvae <295 μm. Further positive identification of late stage *Mytilus* larvae was achieved by examining the hinge teeth of disarticulated valves (Lutz and Hidu 1979).

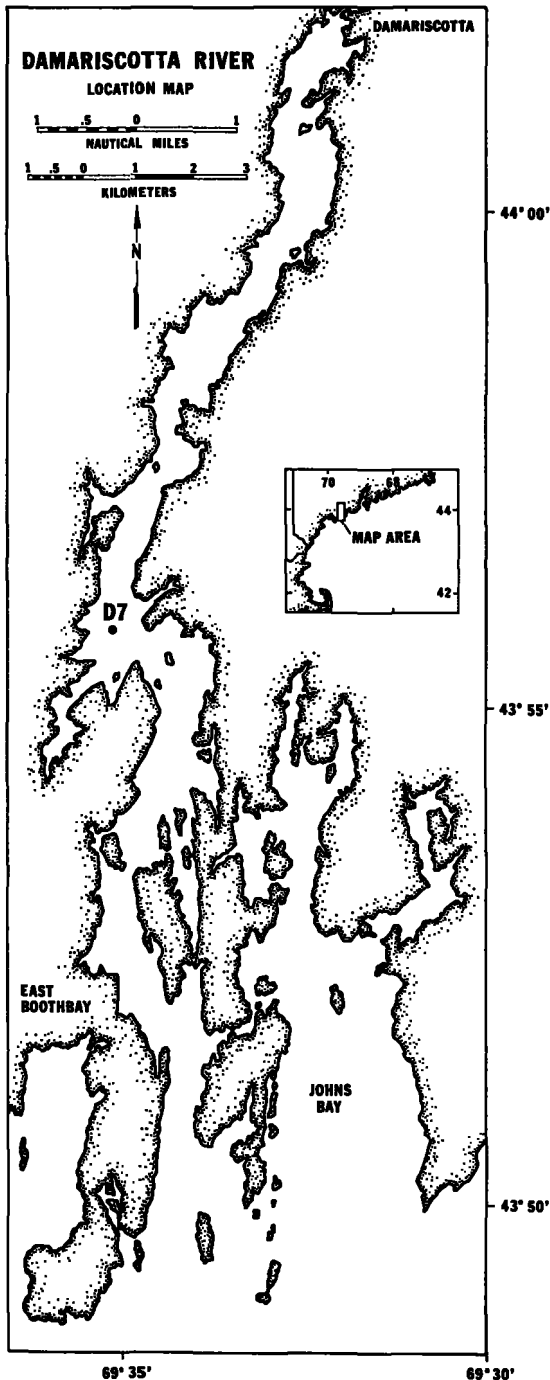Spawning dates were estimated by subtracting the approximate age of the larvae from the sampling

date. Larval age was estimated using photomicrographs of larvae of known age and size for comparison, available in Chanley and Andrews (1971). The initial occurrence of larvae in each year was dominated by early straight hinge larvae. The spawning season was defined by larval abundances >10 m^{-3}. This level was chosen arbitrarily to distinguish major spawning from occasional low larval abundances (<10 m^{-3}).

Environmental variables that were examined for correlations with the initiation of spawning and larval abundance included water temperature, phytoplankton abundance, degree days, calendar date, and lunar cycles. Water temperatures were taken concurrently with the plankton samples. Phytoplankton abundances from July 1974 to August 1977 were available for the Damariscotta River (McAlice unpubl. data). Data from the neighboring Sheepscot River estuary (McAlice and Denniston[3]) were substituted for the period October 1969 to June 1974. The decision to use the Sheepscot data was based on the highly significant Spearman's rank correlation (Zar 1984) ($r = 0.67$, $P < 0.001$) between the Damariscotta and Sheepscot phytoplankton abundances from July 1974 to August 1977. Degree days were calculated in the manner described by Thiesen (1973). For each year, degree days were summed from the time of peak larval abundance the previous year to the initiation of spawning. Lunar cycle information was obtained from tide tables published by NOAA (1969-76).

Results

Examination of the age and abundance of mussel larvae from December 1969 to September 1977 indicated that spawning began in late May or early June when temperatures reached 10°-12.5°C (Fig. 2). The average date when spawning began was 4 June, with a standard deviation of approximately 7 d. The average number of degree days prior to spawning was 2,853, with a standard deviation of 368. No significant relationship was found between degree days and commencement of spawning or degree days and maximum larval abundances.

Commencement of spawning may be related to the time of spring tides (Table 1). In 7 of the 8 yr examined, spawning began within 5 d, before and after, a spring tide. On four occasions spawning commenced within 2 d of a spring tide. Spawning,

once initiated, probably continued throughout the summer as indicated by the persistence of early stage mussel larvae. Spawning appeared to cease as temperatures fell to 9°-14°C in September and October (Fig. 2), when only late stage larvae were present. Maximal larval abundances were observed in mid- to late June, shortly after spawning began. At this time, straight hinge larvae, <6 d old, were dominant. Maximum values for the period 1970-75 ranged from 787 larvae m^{-3} to 5,400 larvae m^{-3}. In 1976 and 1977, maximum abundances were an order of magnitude larger (3.16×10^4 m^{-3} and 6.09×10^4 m^{-3}, respectively). Following the peaks in June, larval densities generally declined through 1 to 3 successively smaller peaks (Fig. 2).

Mussel larvae appeared well after phytoplankton abundances had begun to increase from low winter values to generally high summer values (Fig. 3). Larvae usually disappeared before phytoplankton abundances fell to typically low winter levels.

In addition to the larvae of *Mytilus edulis*, those of *Anomia simplex*, *Geukensia demissa*, *Modiolus modiolus*, and what was probably a complex of *Mya arenaria*, *Hiatella arctica*, and possibly *Sphenia sincera* (Hanks and Packer 1985) larvae were also identified. *Amonia simplex* occurred most commonly from September through December, though never in great numbers. The *Mya-Hiatella-Sphenia* group was often very abundant, and occurred from early May through September. *Geukensia* and *Modiolus* were never common.

TABLE 1.—Estimated dates and temperatures of the initiation and cessation of spawning for *Mytilus edulis* in the Damariscotta River estuary, and dates of nearest spring tides, 1970-77.

Year	Estimated date and (°C) when spawning		Date of nearest spring tide
	began	ended	
1970	2 June (10.0°-13.2°C)	2 Oct. (14.6°-13.9°C)	June 4
1971	8 June (10.2°-12.2°C)	18 Oct. (14.3°-12.8°C)	June 9
1972	16 June (10.5°-12.1°C)	20 Oct. (13.1°-9.0°C)	June 11
1973	12 June (10.0°-14.0°C)	10 Oct. (12.7°-11.0°C)	June 15
1974	12 June (10.7°-12.3°C)	8 Oct. (12.4°-9.1°C)	June 4
1975	27 May (10.3°-12.5°C)	24 Sept. (16.9°-13.7°C)	May 25
1976	24 May (10.1°-12.8°C)	22 Oct. (14.6°-11.0°C)	May 29
1977	2 June (9.3°-10.2°C)	—	June 1

Discussion

A temperature threshold for spawning was indicated by the appearance of *Mytilus* larvae when water temperatures exceeded 10°-12.5°C and the subsequent disappearance of larvae when temperatures fell below 9°-14°C. A number of studies have reported the initiation of spawning in *Mytilus edulis*

[3]McAlice, B. J., and F. D. Denniston. Dominance and diversity of Sheepscot River estuary phytoplankton. Manuscr. in prep. Ira C. Darling Center, University of Maine, Walpole, ME 04573.
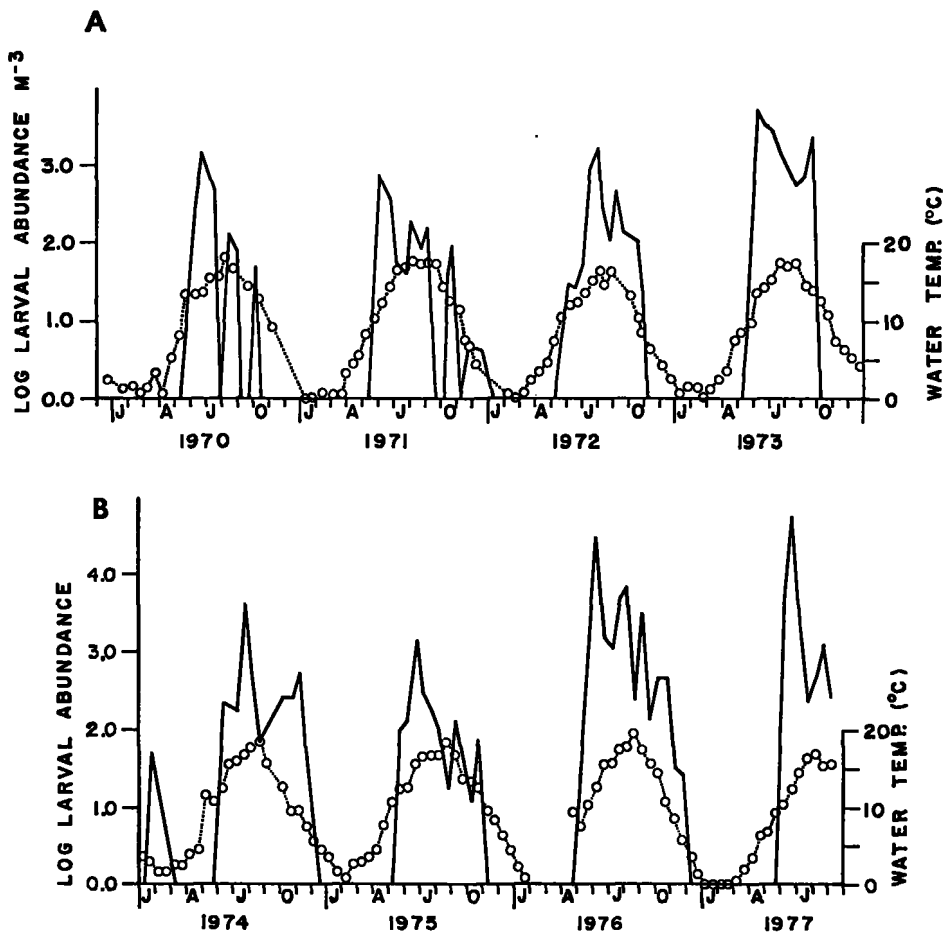
FIGURE 2.—Abundance of *Mytilus edulis* larvae (solid line) and water temperature (broken line) at station D7: A) 1969-73; B) 1974-77.

at temperatures of 10°-13°C or higher while few studies have reported spawning at lower temperatures (Table 2), which also suggests a thermal threshold for spawning. The significance of this threshold may be linked to gametogenesis. Bayne (1965) found that mussels with fully developed gametes would not spawn when held at 5°C under high food concentrations. However, if temperatures were raised to 12°-14°C, gametes matured and spawning ensued. Similarly, Sastry (1968) found that in the bay scallop, *Aequipecten irradians*, oogonia and spermatozoa formed at 15°C and 20°C, but that temperatures higher than 20°C were necessary for oocytes to reach a fertilizable stage. Therefore, the apparent correlation between a particular temperature and the initiation of spawning may actually reflect the maturation of gametes followed by induction of spawning by any of a number of stimuli. Given the predictable rise in temperature each spring, this may explain the initiation of spawning at approximately the same time each year.

Use of degree days to predict the time of spawning does not appear to be useful. This is due to a very regular pattern of rising and falling water temperatures each year. As a result, the sum of degree days between spawning periods conveyed no more information than did elapsed time. Newell et al. (1982) arrived at a similar conclusion for mussel populations in Long Island Sound. They found that one Long Island Sound mussel population spawned 3 mo later than another, despite nearly identical temperature conditions, difference in degree days due solely to a difference in elapsed calendar days. Bayne (1975), however, did find a relationship between rate of gametogenesis and degree days, but not calendar days.
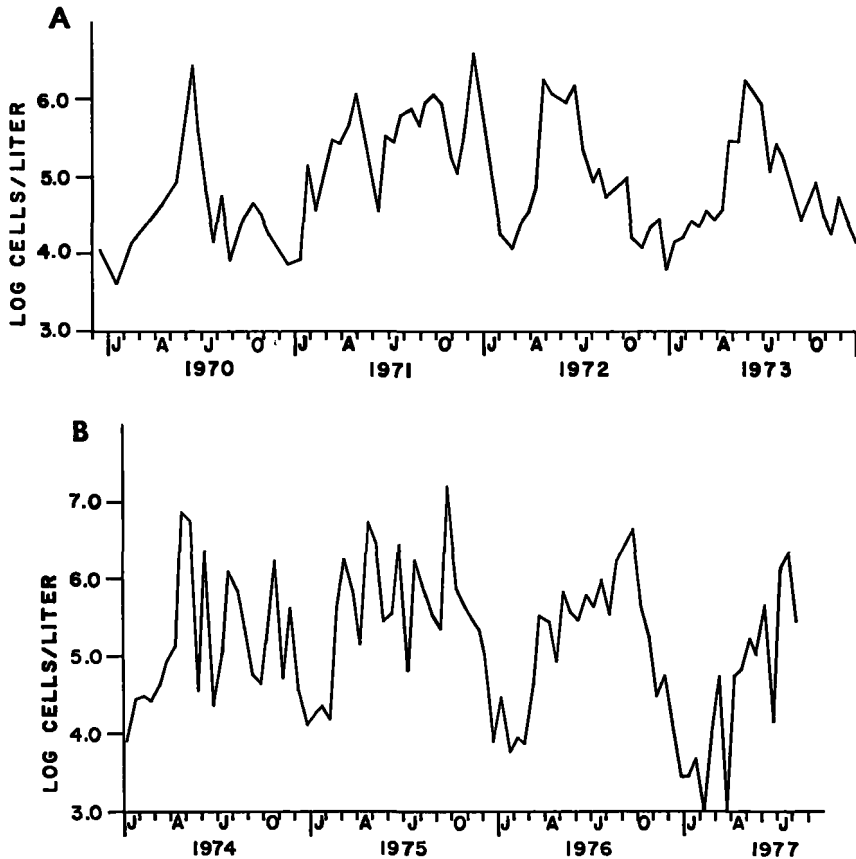
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FIGURE 3.—Abundance of phytoplankton in the lower Sheepscot River estuary: A) 1969-73; B) January 1974-June 1974 and at station D7, July 1974-August 1977.

TABLE 2.—Reported spawning temperatures and periods of *Mytilus edulis*.

Location	Temperatures (°C)	Major spawning period	Reference
Europe			
Norway	8	early May	Bohle 1971
Denmark	7-16	May	Jorgensen 1981
England	9.5-12.5	May	Chipperfield 1953
Sweden	12	mid-May-early June	Kautsky 1982
England	13	early May	Baird 1966
Denmark	13-14	May-June	Rasmussen 1973
United States			
Damariscotta River, ME	10-13	late May-mid-June	This study
Milford, CT	15-16	May	Engle and Loosanoff 1944
Branford, CT	14-16	late May-early June	Fell and Balsimo 1985
Stony Brook, NY	11-15	late April-early June	Newell et al. 1982
Shinnecock, NY	16-22	August-October	Newell et al. 1982

Spawning in response to lunar cycles is also a possibility. Korringa (1947) noted that the European oyster, *Ostrea edulis*, spawns around the period of spring tides and attributed this to increased hydrostatic pressure. Chipperfield (1953) also observed *O. edulis* at several sites in Great Britain shortly after

the occurrence of a spring tide. In our study, spawning began around the time of spring tides, but induction of spawning by hydrostatic pressure has not been reported in mussels. Alternatively, spawning may be induced by other factors associated with spring tides, such as increased temperature fluctuations, air exposure, and water movement. Temperature fluctuations have been shown to induce laboratory spawning in *Mytilus edulis* (Bayne 1976).

While a temperature threshold is suggested, time of year may also be important as indicated by the spawning periods in Table 2. Of the 10 studies examined, all but one reported the initiation of spawning from May to June. Aside from temperature, the initiation of spawning may be influenced by another cyclic phenomena such as photoperiod. Light and photoperiod in particular have been shown to affect the timing of reproduction in a number of marine invertebrates (Segal 1970). While adult mussels are sensitive to changes in light intensity (Bayne et al. 1976), the ability to detect changing photoperiod has not been demonstrated. The results of this study have been attributed to annual temperature cycles, but until light response of mussels is more fully examined photoperiod cannot be ruled out.

Variations in larval abundance from year to year do not appear to be linked to temperature, nor to availability of food energy. Kautsky (1982) reported that Baltic Sea mussel populations were limited to one major spawning by reduced food availability during the remainder of the year. Similarly, Thompson (1979) attributed annual variation in reproductive condition and fecundity of mussels along the coast of Nova Scotia to annual variations in food supply. Bayne (1975) noted that while poor nutrition does not significantly alter the timing of gametogenesis, it can result in resorption of gametes prior to spawning. Newell et al. (1982) suggested that the cycle of food availability could affect both the nutrient storage cycle and the timing of gametogenic events, including spawning. In every year of our study the spring augmentation of phytoplankton was well under way by March or April, with densities $>10^5$ cells 1^{-1}. Significant numbers of mussel larvae were first detected between late May and early June. Thus, it appears that food is not limiting to either adult or larval mussel populations in our area. Our phytoplankton data, however, do not include the smaller naked nanoplankton which, together with particulate organic matter, could account for more than half of the available energy in the Damariscotta River (Incze 1979). This fraction would be a better index of food available to mussel larvae and should be included in studies attempting to link abundance or setting success of larvae to their food supply.

Onset of spawning in Damariscotta River mussel populations is predictable from year to year. It occurs when water temperature exceeds 10°-12.5°C, and near the spring tide portion of the neap-spring cycle. Food does not appear to be limiting to either gametogenesis or the development of larvae.

Literature Cited

BAIRD, R. H.
  1966. Factors affecting the growth and condition of mussels (*Mytilus edulis* L.). Fish. Invest., Lond., Ser. II, 25:1-33.
BAYNE, B. L.
  1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1-47.
  1975. Reproduction in bivalve molluscs under environmental stress. In F. J. Vernberg (editor), Physiological ecology of estuarine organisms, p. 259-277. Univ. South Carolina Press.
  1976. The biology of mussel larvae. In B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 81-120. Cambridge Univ. Press, N.Y.
BAYNE, B. L., J. WIDDOWS, AND R. J. THOMPSON.
  1976. Physiology II. In B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 207-260. Cambridge Univ. Press, N.Y.
BOHLE, B.
  1971. Settlement of mussel larvae *Mytilus edulis* on suspended collectors in Norwegian waters. 4th Eur. Mar. Biol. Symp., p. 63-69.
CHANLEY, P., AND J. D. ANDREWS.
  1971. Aids for identification of bivalve larvae of Virginia. Malacologia 11:45-119.
CHIPPERFIELD, P. N. J.
  1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. J. Mar. Biol. Assoc. U.K. 32:449-476.
DESCHWEINITZ, E. H., AND R. A. LUTZ.
  1976. Larval development of the northern horse mussel, *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* (L.) as an aid in planktonic identification. Biol. Bull. (Woods Hole) 150:348-360.
ENGLE, J. B., AND V. L. LOOSANOFF.
  1944. On season of attachment of larvae of *Mytilus edulis*. Ecology 25:433-440.
FELL, P. E., AND A. M. BALSAMO.
  1985. Recruitment of *Mytilus edulis* L. in the Thames estuary, with evidence of differences in the time of maximal settling along the Connecticut shore. Estuaries 8:68-75.
FIELD, I. A.
  1922. Biology and economic value of the sea mussel *Mytilus*

edulis. Fish. Bull., U.S. 38:127-260.

FROLANDER, H. F.
1968. Statistical variation in zooplankton numbers from sub-sampling with a Stempel pipette. J. Water Pollut. Control Fed. 40:R82-R88.

HANKS, R. W., AND D. B. PACKER.
1985. A new species of *Sphenia* (*Bivalvia:Myidae*) from the Gulf of Maine. Veliger 27:320-330.

INCZE, L. S.
1979. Relationships between environmental temperatures, seston, and the growth and survival of *Mytilus edulis*, L. in a north temperate estuary. M.S. Thesis, Univ. Maine, Orono.

JORGENSON, C. B.
1981. Mortality, growth and grazing impact of a cohort of bivalve larvae, *Mytilus edulis.* (L.). Ophelia 20:185-192.

KAUTSKY, N.
1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. Mar. Biol. (Berl.) 58:143-160.

KORRIGA, P.
1947. Relations between the moon and periodicity in the breeding of marine animals. Ecol. Monogr. 17:347-381.

LEE, W. Y., AND B. J. MCALICE.
1979. Sampling variability of marine zooplankton in a tidal estuary. Estuarine Coastal Mar. Sci. 8:565-582.

LOOSANOFF, V. L., H. C. DAVIS, AND P. E. CHANLEY.
1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia 4:351-435.

LOOSANOFF, V. L., AND C. A. NOMEJKO.
1951. Existence of physiologically different races of oysters, *Crassostrea virginica.* Biol. Bull. (Woods Hole) 101:151-156.

LUTZ, R. A., AND H. HIDU.
1979. Hinge morphogenesis in the shells of larval and early post-larval mussels (*Mytilus edulis* and *Modiolus modiolus* L.). J. Mar. Biol. Assoc. U.K. 59:111-121.

MCALICE, B. J.
1977. A preliminary oceanographic survey of the Damari-scotta River estuary, Lincoln County, Maine. Maine Sea Grant Tech. Rep. 13, 27 p.

NEWELL, R. I. E., T. J. HILBISH, R. K. KOEHN, AND C. J. NEWELL.
1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (*Bivalvia, Mytilidae*) from localities on the east coast of the United States. Biol. Bull. (Woods Hole) 162:299-310.

NOAA.
1969-1976. Tide Tables: East Coast of North and South America, including Greenland. Tide Tables Natl. Ocean Surv. (U.S.) 1969-1976.

RASMUSSEN, E.
1973. Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. Ophelia 11:1-495.

SASTRY, A. N.
1968. The relationships among food, temperature and gonad development of the bay scallop, *Aequipecten irradians* Lamarck. Physiol. Zool. 41:44-53.

SEED, R.
1975. Reproduction in *Mytilus* (*Mollusca:Bivalvia*) in European waters. Publ. Stn. Zool. Napoli 39(suppl. 1):317-334.

SEGAL, E.
1970. Light, animals, invertebrates. *In* O. Kinne (editor), Marine ecology, Vol. I, Part I, p. 159-211. Wiley-Interscience, N.Y.

STAUBER, L. A.
1950. The problem of physiological species with special reference to oysters and oyster drills. Ecology 31:109-118.

STUBBINGS, H. G.
1954. The biology of the common mussel in relation to fouling problems. Research 7:222-229.

THEISEN, B. F.
1973. The growth of *Mytilus edulis* L. (*Bivalvia*) from Disko and Thule district, Greenland. Ophelia 12:59-77.

THOMPSON, R. J.
1979. Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*), the sea urchin (*Stronglyocentrotus droebachiensis*) and the snow crab (*Chionocetes opilio*) from populations in Nova Scotia and Newfoundland. J. Fish. Res. Board Can. 36:955-964.

ZAR, J. H.
1984. *Biostatistical analysis.* 2d ed. Prentice-Hall, Englewood Cliffs, N.J.

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