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Field and laboratory observations of spawning periodicity and behavior of a northern population of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae)*

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Synopsis

The spawning periodicity and mating behavior of a northern population of the Atlantic silverside, *Menidia menidia*, was studied both in the field (Salem Harbor, Massachusetts) and in laboratory experiments. Spawning in the field coincided with new and full moons. Under conditions of unlimited food availability in artificial outdoor pools that received natural celestial illumination or in indoor aquaria receiving no evening illumination, spawning occurred every 1-3 days rather than fortnightly. These results suggest that tidal influences are a primary factor that synchronizes spawning in *M. menidia*. Published reports of diel time of spawning in both marine and freshwater species of *Menidia* indicate a generic tendency to spawn during mid-morning. This pattern coupled with high tides that cover suitable spawning substrates during mid-morning only at fortnightly intervals could account for the semilunar spawning cycle in marine populations of *Menidia*. Although general characteristics of the reproductive ecology of *M. menidia* in Massachusetts were similar to a thoroughly studied population in South Carolina, several differences were evident. The breeding season was shorter in Massachusetts (late April-June), and occurred over a much lower range of temperatures (9-21°C). Intensity and frequency of spawning was correlated with the height of high tide. Eggs were deposited only on mats of intertidal, filamentous algae rather than on roots or stems of *Spartina alterniflora* or other intertidal vegetation. Promiscuous spawning occurred in small, highly male-dominated groups of fish, primarily after the tide had begun to recede, and often at the water's edge. No predation on spawning adults was observed but the mummichog, *Fundulus heteroclitus*, fed daily on developing embryos during high tide.

Introduction

Regularly recurring environmental events strongly influence the timing of reproductive cycles in a wide variety of marine organisms (Enright 1975, Gibson 1978, Scott 1979). Recently, attention has focused on identifying lunar and semilunar spawning rhythms in fishes: Johannes (1978) listed 51 species known to have lunar-related spawning cycles and several more have since been discovered (e.g., Taylor et al. 1979, May et al. 1979, Pressley 1980, Middaugh 1981). However, environmental

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cues that synchronize lunar reproductive rhythms in fishes are not clearly understood, largely because manipulative experiments on the spawning periodicity of most fishes are difficult. Furthermore, in some fishes, the adaptive significance of lunar-related reproductive rhythms is difficult to unambiguously define.

Laboratory experiments have demonstrated that lunar spawning periodicities are synchronized by lunar illumination and/or an endogenous cycle in several marine invertebrates (e.g., the polychaete, *Platynereis dumerili*, Hauenschild 1960; the midge, *Clunio marinus*, Neumann 1966). In fishes, it has also been proposed that endogenous and lunar factors interact to synchronize spawning (Gibson 1978, Enright 1975), but experimental evidence is often lacking. For instance, it has not been clearly determined whether the well-known, semilunar spawning cycle of the California grunion, *Leuresthes tenuis*, is mediated directly by a lunar stimulus, indirectly through lunar-related stimuli such as fortnightly fluctuations in tidal height, an endogenous component involving egg maturation, or a combination of the above (Walker 1949, 1952, Korringa 1957, Scott 1979).

Discussions of the adaptive significance of lunar spawning cycles are tautological if based on the assumption that because a rhythm exists, it must be adaptive. One way of elucidating the adaptive value of a spawning rhythm is to examine how different selective factors prevailing in different habitats alter the timing and behavioral characteristics of reproduction between conspecific populations. As Johannes (1978) asserted: 'It would be wrong to infer that the timing or location of spawning described for a species on the basis of studies in a single area is invariable throughout its range'. For example, the mummichog, *Fundulus heteroclitus*, displays a lunar reproductive rhythm in southern portions of its range (e.g., Delaware Bay, Taylor et al. 1979) which it reportedly lacks at more northern latitudes (e.g., Woods Hole, Massachusetts, Wallace & Selman 1981). Other aspects of the reproductive ecology of *F. heteroclitus* are also known to vary geographically (Able & Castagna 1975).

The Atlantic silverside, *Menidia menidia*, is a common estuarine fish of the eastern North American coast, ranging from the Magdalen Islands, Quebec, Canada to northern Florida (Gosline 1948, Johnson 1975). The life span of *Menidia* is completed in one year (Bayliff 1950, Conover & Ross 1982); breeding occurs from March to July at southern latitudes (Middaugh & Lempesis 1976) and from April or May to July at northern latitudes (Bigelow & Schroeder 1953, Conover & Ross 1982). Middaugh (1981) and Middaugh et al. (1981) provided a thorough description of the semilunar spawning cycle, sites of intertidal egg deposition, and mating behavior of a population of *M. menidia* from South Carolina. The purposes of the present paper are twofold: (1) to present field evidence demonstrating that semilunar spawning rhythms also occur in a northern population of *M. menidia* at Salem Harbor, Massachusetts, and experimental evidence suggesting that such rhythms are not synchronized solely by celestial cues or an endogenous clock; and (2) to describe the timing of spawning, egg deposition sites, and mating behavior of *M. menidia* in Massachusetts. An analysis of fecundal patterns in this serial spawner will be provided in a later paper.

Methods

Study site

All field observations were conducted from the shoreline of a small cove at the head of Salem Harbor, Massachusetts, near the entrance of the Forest River (a salt marsh creek). This cove is characterized by an extensive intertidal mudflat, fringed in the upper intertidal zone by a narrow band (5-10 m) of cordgrass (*Spartina alterniflora*) and short stretches of pebble. The southern shore of this cove was identified as a major spawning site for *M. menidia* during a survey conducted in spring 1978.

Field observations

From May 1 to July 15, 1979, we conducted daily observations of the sites of egg deposition, timing and intensity of spawning activity, and mating behavior of *M. menidia* during a 3 h period bracketing the time of daytime high tides. The intensity of spawning activity was measured during three 1 h intervals relative to the predicted time of high tide (HT): 1) a pre-HT interval, 1.5-0.5 h prior to HT; 2) the HT interval, 0.5 h before to 0.5 h after HT; and 3) a post-HT interval, 0.5-1.5 h after HT. Our measure of spawning intensity consisted of counting the number of aggregations of *Menidia* engaged in spawning as an observer (the senior author) walked a standard length of shoreline (75 m) at a constant rate. These aggregations consisted of 5-10 to as many as several hundred fish and were distributed along the shoreline within 3 m of the water's edge. Counts were made twice (about 0.5 h apart) during each interval. Storms prevented observations on May 17, 20, and 30 but examination of spawning substrates for new eggs indicated that no spawning had occurred. Water temperatures were continuously recorded with a Ryan thermograph and salinities were measured at high tide with a YSI salinometer.

Mating behavior was observed directly in the field and from motion picture films made with a Super-8 movie camera when weather permitted. All field observations were tape recorded. We made additional observations intermittently during 1980 to confirm patterns identified in 1979. At the same site, we concurrently observed the spawning activity and egg deposition sites of another intertidal spawner, *Fundulus heteroclitus*.

Laboratory experiments

All laboratory experiments were conducted at the University of Massachusetts Marine Station, Gloucester, Massachusetts. To examine the persistence of semilunar spawning rhythms under laboratory conditions, we introduced two male and one female *M. menidia* captured from Salem Harbor into each of four, 74 l tanks (75 × 32 × 31 cm) on May 5, 1979. We maintained these fish indoors at room temperature on a natural photoperiod but with no evening illumination.

To determine the influence of celestial cues on spawning rhythmicity, we introduced four male and four female *Menidia* on May 5, 1979, into each of two circular, plastic pools (diameter 1.5 m, depth 0.3 m) located outdoors where they received natural, celestial illumination. Pools were shielded from ground-level sources of light and about 25% of the surface area was shaded from direct sunlight. One pool was elevated slightly above the other and a slow, circular flow of seawater was provided in each pool by pumping seawater between pools and providing a gravity-feed return.

All fish were fed chopped, fresh seaworms (*Nereis* sp.) to excess daily, and wild-caught, live amphipods intermittently. Seawater in each aquarium or pool was vigorously aerated and replaced every 3-5 days. To provide a spawning substrate, we anchored a small tuft of synthetic, aquarium filter-floss to the bottom of each aquarium or pool and checked it several times daily for the presence of eggs. When no other similar substrate is available, *M. menidia* consistently spawns on filter-floss.

We estimated the time of day that spawning had occurred in the following manner. First, cell division rates for the first few hours of egg development were determined at three different temperatures (Fig. 1). Thereafter, each time eggs were discovered, the water temperature was recorded and egg development stage observed under a dissecting microscope. We then estimated the time of spawning (±2 h) graphically from Figure 1. The eggs were preserved and later enumerated. A new tuft of filter-floss was immediately introduced into aquaria or pools.

Atlantic silversides display no visually perceptible sexual dimorphism except that females are slightly larger than males. Hence, it was necessary to verify that spawning behaviors ascribed to males and females in the field were, in fact, correct. We accomplished this by introducing only large females (110-120 mm total length) and small males (84-96 mm total length) into the outdoor pools so that sex could be easily identified by size. We then compared observations of male and female spawning behavior in the pools with observations in the field.

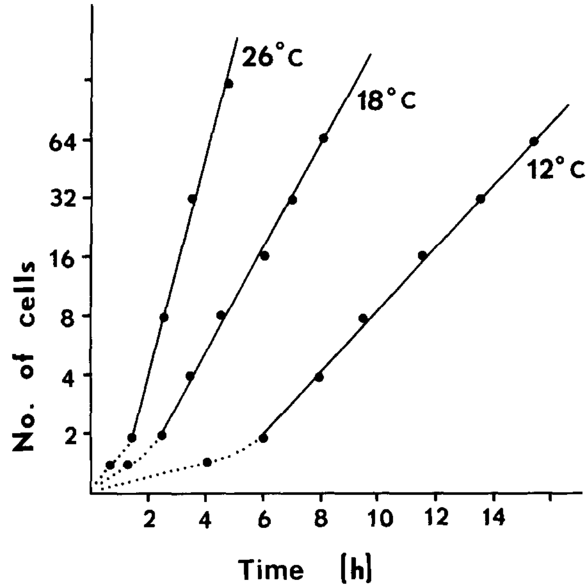

Fig. 1. Rate of development of eggs of *Menidia menidia* at three temperatures during the first few hours after fertilization.

Results

Spawning periodicity in the field

Spawning of *M. menidia* in Salem Harbor during 1979 was highly periodic and coincided with the occurrence of new and full moons (Fig. 2). As evidenced by the appearance of eggs in the field, the spawning season began with the new moon in late April (before we began quantitative observations) at water temperatures of 9-12°C. Spawning ended with the new moon in June, at water temperatures of 19-21°C, after five fortnightly spawning phases. During the spawning phases in May, emerging shoots of *Spartina* were relatively short (1-5 cm) but by late June, they were much taller (5-50 cm). Hence, the lower number of spawning groups sighted during June spawning phases may have been partly because visibility to the observer was reduced. A high proportion of the total spawning activity during semilunar breeding phases occurred on a single day: 40% of all spawning groups enumerated near the full moon phase in May were observed on May 12; 90% on May 22 of a new moon phase; 65% on June 14 of a full moon phase; and 50% on June 26 of a new moon phase. Despite continued observation, no spawning activity was detected in July.

The occurrence of spawning was influenced by tidal height (Fig. 3), as might be expected, since semilunar and tidal mechanics are linked. Spawning never occurred on days when the daytime tidal height was <2.8 m, thus excluding 33% of all daytime high tides. Contingency table analysis of these data (Fig. 3) supported the conclusion that frequency of spawning was dependent on tidal height $\chi^2=14.5$, $p<0.025$). Intensity of spawning, as measured by number of observed spawning groups, was also highly correlated with tidal height (Spearman's Rank Correlation: $n=61$, $r=0.38$, $p=0.003$). Salinities varied irregularly from 24 to 28‰ during the spawning season and did not correspond with spawning patterns.

Spawning intensity was greatest after the tide had begun to recede. Of 142 total spawning groups enumerated during daily assessments of spawning intensity, 11 occurred during the pre-HT interval, 11 during the interval bracketing HT, and 120 during the post-HT interval. Spawning activity occasionally continued up to 2 h 30 min after HT. No spawning was observed at night.

Spawning substrates

Atlantic silversides used only filamentous, intertidal algae as spawning substrates. During May, eggs were deposited in luxuriant mats of the brown alga, *Pilayella littoralis*, that were prevalent in the upper intertidal zone, and growing over and amongst emerging shoots of *Spartina*. By June, these mats of *Pilayella* had declined and *Menidia* then used mats of *Enteromorpha* sp. that began growing amongst *Spartina* in the upper intertidal zone. Eggs were attached by numerous threads to the base or underside of these algal mats, which afforded protection from direct sunlight and desiccation. Despite the presence of other intertidal vegetation such as *Ulva lactuca, Ascophyllum nodosum, Fucus vesiculosus, Chondrus crispus,* and *Spartina alterniflora,* only *Pilayella* and *Enteromorpha* were used as spawning substrates. However, only *Pilayella, Enteromorpha,* and

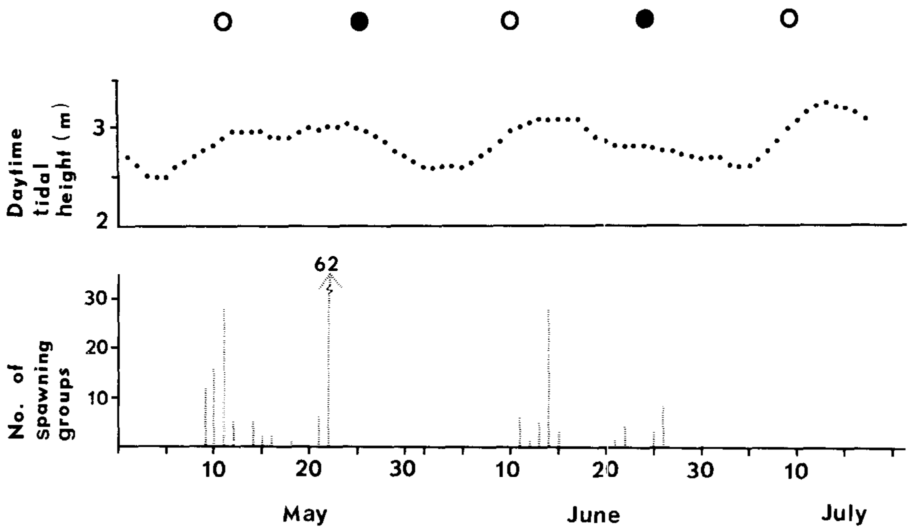

Fig. 2. Lunar phase, daytime tidal height, and number of spawning groups of Atlantic silversides enumerated during daily assessments of spawning intensity at Salem Harbor, Massachusetts during 1979. Open circles represent full moons and shaded circles new moons. When two high tides occurred during daylight hours, tidal height of the morning tide was plotted.

Spartina were abundant in the upper intertidal zone: the other species occurred mainly in the mid-intertidal zone. Algal mats of *Pilayella* and *Enteromorpha* were especially prevalent at our study site and may explain the intensive use of this area as a spawning location.

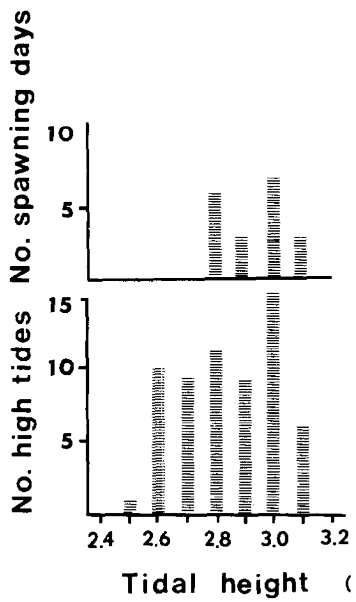

Fig. 3. Number of daytime high tides by tidal height during the spawning season of *Menidia menidia* and number of spawnings by tidal height during the spawning season.

Spawning periodicity in the laboratory

Of the four females placed in individual indoor aquaria, only two fed actively and initiated spawning (Fig. 4). Female A spawned a total of 20 times over the period May 11 to July 22 and died several hours after its final spawning session; most spawning occurred after vigorous feeding began on about May 28. Female C began feeding vigorously shortly after the experiment began and spawned seven times from May 11 until it died on June 9 after jumping out of the aquarium. The two groups of fish in the outdoor pools began active feeding about May 16. Spawning began shortly thereafter and continued until July 22 (Fig. 4). Unlike natural spawning rhythms in the field, spawning in indoor aquaria and outdoor pools occurred every 1-3 days rather than on a fortnightly cycle coincidental with new and full moons. Spawning occurred at water temperatures of 13 to 24° C.

Most spawnings in indoor aquaria and outdoor pools occurred near sunrise or sunset (Fig. 5), perhaps because light intensity and disturbance by observers were reduced at such times. During midday, the fish rarely left the shaded portion of the pools.

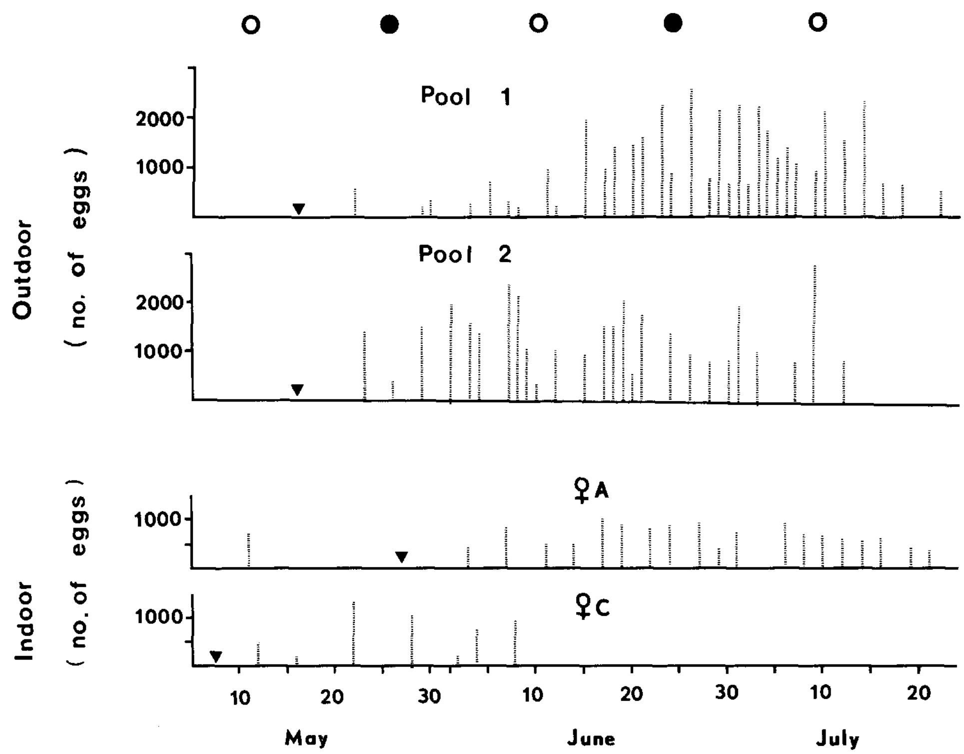

Fig. 4. Number of eggs spawned in outdoor pools where Atlantic silversides received natural celestial cues and indoor aquaria that received no evening illumination. Outdoor pools each contained four males and four females and indoor aquaria each contained two males and one female. The solid triangle indicates the date when the fish in each treatment began actively feeding. Open circles represent full moons and shaded circles new moons. The experiment began May 5 and was terminated July 27.

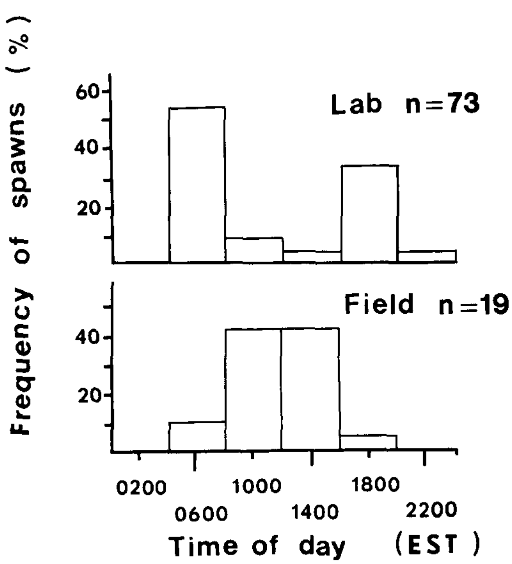

Fig. 5. Time of day that spawning of *Menidia menidia* occurred in the field at Salem Harbor and in experimental aquaria (indoor and outdoor) in 4 h intervals expressed as a percentage of the total number of spawnings (n) that occurred.

Mating behavior

The mating behavior of *M. menidia* in outdoor pools proceeded as follows. All males and one or more females began repeatedly circling the perimeter of the pool in a group, frequently passing close to the spawning substrate. Soon, males began vigorously pursuing a female (or females) and nudging or nipping (seemingly) at her vent. As a ripe female (or females) approached the spawning substrate, pursuit and nudging by males became especially vigorous. Females often darted away from the males whereupon the process began anew. Eventually, a ripe female either passed partly through the filter-floss or turned on her side along the outer base of the filter-floss, and released eggs with a rapid quivering of the abdomen and tail during a 5 to 15 second period. Usually all four males followed immediately behind the female and, with a rapid quivering, released milt. Non-ripe females (as evidenced by a lack of abdominal swelling) took no part in the spawning activity. We observed no aggressive interactions between or among individuals of either sex.

Spawning behavior in the field was similar to that observed in the laboratory. Usually one or two large schools appeared at the spawning site 1½ h before to 1 h after HT and swam back and forth very close to shore where algal mats were present. As the tide began to recede, smaller groups of fish dispersed from large schools and began circling individual clumps of algae. Numerous males then began pursuing and nudging individual females, culminating in release of gametes. Groups of fish sometimes swam to the water's edge to spawn. On many occasions, spawning did not occur until only about 1 cm of water remained over the algal mats; the bodies of some fish broke the surface of the water as spawning proceeded.

During spawning, isolated spawning schools of 5 to 50 fish could be easily captured with a dip-net. Thus, we verified that spawning groups were composed of many more males than females (average about 10:1, see Table 1 in Conover 1984). On one occasion, several females spawned in concert with up to 100-200 males and the water column became whitened from the milt. We did not observe one-to-one pairing of males and females. Hence mating in *M. menidia* is truly promiscuous.

Spawning and predation by Fundulus heteroclitus

Fundulus heteroclitus spawned on the same algal mats as *Menidia* and eggs of both species were often noted side by side. Numerous *Fundulus* were present at the study site and some spawning was observed nearly every day from mid-May to July. Although we made no quantitative measure of spawning intensity, a lunar pattern was not evident. Like *Menidia, Fundulus* appeared to commence spawning as the tide began to recede and algal mats were barely submerged. Spawning was confirmed by presence of eggs that were not yet water-hardened immediately after high tide. Field observations suggested that *Fundulus* also spawned at night.

Table 1. Percent frequency occurrence and mean number of eggs in digestive tracts of adult *Fundulus heteroclitus* collected during high tide at Salem Harbor, Massachusetts. The number of adult *F. heteroclitus* examined is noted (N).

		Eggs of *Menidia*		Eggs of *Fundulus*	
Date	N	% Occurrence	Number ($\bar{x}$)	% Occurrence	Number ($\bar{x}$)
5/ 9/79	20	45	6.5	20	1.8
5/10/79	24	62	13.3	25	3.3
5/31/79	20	45	9.7	25	17.4
6/14/79	11	73	30.0	45	4.4

Fundulus preyed on both its own eggs and those of *Menidia* during periods of high tide (Table 1). Examinations of the digestive tracts of *F. heteroclitus* collected during high tide at Salem Harbor on four occasions indicated that 45-73% contained eggs of *Menidia* and 20-45% contained eggs of *Fundulus*.

Discussion

Spawning periodicity

In our experiments, a fortnightly spawning rhythm did not persist in a laboratory environment that excluded tidal influences, whether natural celestial cues were provided (outdoor pools) or not (indoor aquaria). These data suggest that the lunar-related reproductive rhythm in *M. menidia* is not maintained by celestial cues alone. The experimental results further suggest that an endogenous cycle of fortnightly spawning does not persist when individuals are removed from their natural habitat. However, our experimental fish required a lengthy period of adjustment to laboratory conditions (3-23 days as evidenced by initiation of active feeding) that may have disrupted endogenous rhythms. Nevertheless, our experiments showed that Atlantic silversides are physiologically capable of spawning much more often than fortnightly. Our field observations showed that spawning frequency and intensity were both correlated with tidal height. Therefore, lunar-related tidal cycles may be the primary factor synchronizing reproduction in natural populations of *M.*

menidia, although celestial and endogenous factors could interact with tidal regimes to produce the fortnightly reproductive pattern observed in the field.

The effect of tidal cycles on spawning periodicity could be mediated in several ways. For instance, Gilmurray & Daborn (1981) showed that *M. menidia* fed primarily during ebb tide in the Bay of Fundy and suggested that tidal movements influence the temporal utilisation and availability of food. Hence, tidal cycles and feeding dynamics of *M. menidia* are linked in nature. In our laboratory experiments, *M. menidia* spawned much more frequently than in the field, perhaps because of the unlimited food that was continuously available to them. Correspondingly, the total number of eggs produced by laboratory females was much higher than estimates of total fecundity for individuals in the field (70-130 eggs mm^{-1} body length in the lab as compared to about 45 eggs mm^{-1} body length in the field, determined by multiplying batch fecundity by spawning frequency; Conover 1979 and unpublished data). In natural populations, spawning periodicity could be partly determined by rate of egg production as it interacts with tidally-mediated availability of food and spawning habitat.

The time of day when high tide occurs could also be an important factor that limits spawning to semilunar periods. Middaugh (1981) suggested that the occurrence of a high tide at sunrise on days immediately preceding the new and full moon could synchronize spawning because high tides at sunrise occurred with a periodicity similar to that of spawning. However, we believe the fortnightly spawning periodicity of *M. menidia* may be explained more simply. Middaugh reported that the median time of spawning in *M. menidia* from South Carolina was 1051 h (EST). In our study, the weighted mean time of high tide on days of spawning (weighted by spawning intensity on that day) was 1026 h (EST). According to Hubbs (1976), a freshwater population of the silverside, *Menidia beryllina* (= *Menidia audens*, Chernoff et al. 1981), also spawns only during mid-morning in Lake Texoma, Texas; the greatest incidence of spawning activity being at 1000 h Fisher (1973) also observed *M. beryllina* spawning during mid-morning hours in a California reservoir. This similarity in diel time of spawning for both freshwater and marine species of *Menidia* suggests a generic tendency to spawn during mid-morning, irrespective of tidal influences.

Many marine fishes are known to spawn only at a specific time of day (see Ferraro 1980). If time of day is a primary factor then the simplest explanation for the semilunar spawning cycle of *M. menidia* may be that suitable spawning substrates are covered by water during mid-morning only at fortnightly intervals. Correspondingly, freshwater populations of *M. beryllina* spawn daily (Hubbs 1976) as would be expected where spawning substrates are continuously available. This hypothesis could be tested by comparing the spawning periodicities of populations of *M. beryllina* in tidal environments such as estuaries with those in landlocked freshwater populations.

The adaptive value of spawning at a specific time of day is unknown in most fishes but could involve diel physiological rhythms of feeding and egg maturation. Taylor et al. (1979) showed that the spawning periodicity of *Fundulus heteroclitus* involved a diel physiological rhythm of egg maturation superimposed over a lunar spawning cycle. In *M. menidia*, the digestive tracts of fish captured during spawning runs were consistently empty and pressed flat by swelling of the gonads (personal observations). By spawning in the morning, fish could feed on the ebb tide in the afternoon. A diel cycle might involve spawning in the morning, feeding in the afternoon, and gonadal hydration at night. The problem with our hypothesis of mid-morning spawning is that the experimental fish did not spawn only in the morning, but tended to spawn near the time of sunrise or sunset. However, this deviation could simply have been an artifact of laboratory confinement, most notably the continuous availability of spawning substrates and unlimited food, lack of tidal cues, and disturbances caused by human activity. Furthermore, light intensity may have also disturbed the experimental fish because they rarely left the shaded portion of the pools during midday.

Geographic variation

Many characteristics of the reproductive ecology of *M. menidia* appear to differ between populations at northern and southern latitudes. Middaugh (1981) demonstrated that a population of *M. menidia* in the North Edisto River estuary of South Carolina reproduced on a semilunar cycle involving 6-8 spawning phases. Spawning began in March at water temperatures of 16-20° C and continued until June or July when water temperatures reached 20-30° C. Time of day when spawning occurred corresponded closely with and bracketed the time of high tide. The present study confirms that Atlantic silversides also spawn on a semilunar cycle in Massachusetts, but other characteristics differ. The breeding season in Massachusetts was much shorter, beginning in late April but ending about the same time as in South Carolina. (Although we did not observe or detect spawning in July, we collected ripe fish in July.) Spawning occurred over a much lower temperature range in Massachusetts (9-21° C). It is perhaps surprising that the breeding season does not extend longer in Massachusetts, considering that water temperatures are still relatively moderate in July. However, the length of the growing season for juveniles is also probably shorter in Massachusetts. Conover & Ross (1982) have demonstrated that winter mortality at northern latitudes is size-selective: few individuals less than 85 mm in total length survive the winter. Were the breeding season to extend into July or August, these offspring would probably have little chance of surviving the winter.

Middaugh et al. (1981) reported that, in South Carolina, eggs of *M. menidia* were deposited in the upper intertidal zone, directly on stems of *Spartina alterniflora*, or on the roots where exposed by erosion or the burrowing activities of crabs. Detrital mats composed of decaying *Spartina* debris were also frequently used for depositing eggs. In contrast, Atlantic silversides in Massachusetts exclusively used filamentous, intertidal algae as spawning substrates, despite the presence of other intertidal vegetation, including *Spartina*. However, Moore (1980) described one spawning by *M. menidia* on algal mats attached to a floating dock in the Beaufort River, South Carolina.

Differences in mating behavior also exist between northern and southern populations. Middaugh et al. (1981) reported that there was a continuous change in position of individuals within schools of *Menidia* just before spawning, with fish from the offshore lateral flank constantly moving to a leading position. Spawning was initiated by a few fish moving into the uppermost intertidal zone. Spawning often occurred in large schools so densely packed that oxygen depletion resulted and visible whitening of the water occurred in an area as large as 75-100 m^2 adjacent to shore. Time of day when spawning occurred corresponded closely with the precise time of high tide. However, we never observed 'leaders' in prespawning schools. Instead, we observed that large prespawning schools broke up into many smaller aggregations of a few females and numerous males. Spawning was initiated by vigorous pursuit and abdominal nudging of females by several males. We observed discoloration of the water column on only one occasion and even that was slight. Moreover, most spawning in Massachusetts occurred as the tide ebbed.

Middaugh et al. (1981) also described several other variations of spawning behaviors ascribed to males and females but they did not state how the sexes were distinguished in the field. We found it difficult to positively identify the sexes in the field, but verified our observations in the laboratory where males and females could be discerned. By netting spawning aggregations, we also noted that mating groups were highly male-dominated (Conover 1984). Middaugh et al. (1981) did not provide data on the sex ratios of spawning schools in South Carolina but the frequent whitening of the water column by spawning schools suggests a high proportion of males. However, Moore (1980) found that the sex ratio of one spawning school in South Carolina was near unity.

Several of the geographic differences in reproductive ecology and behavior of *M. menidia* may result from differences in predation pressure on embryos and adults. Middaugh (1981) listed 16 predators observed feeding on spawning schools of Atlantic silversides in South Carolina (especially bluefish *Pomatomus saltatrix*, and spotted seatrout, *Cynoscion nebulosus*, whereas we observed no predators on breeding groups. In South Carolina, the movement of members of a school from the offshore lateral flank to a leading position and the tendency to remain in large schools while spawning may represent a response to predation on breeding adults. Conversely, Middaugh (1981) noted only occasional predation on embryos (primarily by the blue crab, *Callinectes sapidus*, but we found predation on embryos by *F. heteroclitus* to be a daily occurrence. Hence, in Massachusetts the tendency of *M. menidia* to spawn at the extreme water's edge as the tide recedes may be an adaptive response that reduces the time available for *Fundulus* to prey on eggs and embryos. *Menidia* eggs are especially sensitive to predation immediately after being spawned, i.e., before the adhesive threads have become entangled in algal mats and before the eggs have water-hardened (0.5-1.0 h after spawning, personal observations). Water-hardened eggs are capable of passing through the digestive tract of mummichogs intact (Conover, unpublished data), and Middaugh (1981) reported that viable embryos could pass through the digestive tract of a bird, the ruddy turnstone, *Arenaria interpres morinella*. Our observations that *F. heteroclitus* preys on eggs of conspecifics and also spawns at the water's edge as the tide recedes accords with the hypothesis that such behavior is a means of reducing predation on eggs.

Geographic variation in reproductive ecology also exists among populations of *Fundulus heteroclitus* along the eastern North American coast and may include the existence of lunar-related spawning cycles. Taylor et al. (1979) showed that a population of mummichogs from Delaware displayed a lunar-related spawning cycle, but Wallace & Selman (1981) reported that populations of *F. heteroclitus* from the Woods Hole, Massachusetts, region spawned continually through the breeding season. Our qualitative observations of daily spawning in *F. heteroclitus* are similar to those of Wallace & Selman (1981) but do not rule out the possibility of a lunar peak in spawning. Like populations of *Menidia*, populations of *F. heteroclitus* also differ in sites of egg deposition: a Delaware population spawns on the inner surface of the primary leaves of *Spartina* (Taylor et al. 1977), a Virginia population deposits eggs in empty shells of the ribbed mussel, *Modiolus demissus* (Able & Castagna 1975), and Connecticut and Massachusetts populations spawn on intertidal algal mats (Pearcy & Richards 1962 and present study). The egg morphology of *F. heteroclitus* also varies geographically: in egg diameter, thickness of the chorion, and existence of chorionic fibrils (Brummett 1966, Able & Castagna 1975, Wallace & Selman 1981).

Are differences in reproductive patterns between northern and southern populations of *M. menidia* genetically based? Morgan & Ulanowicz (1976) demonstrated electrophoretically that northern and southern populations of *Menidia* differ in a muscle protein polymorphism that corresponds to a phenotypic difference in body depth. We suggest that the reproductive patterns of marine fishes such as *Menidia menidia* and *Fundulus heteroclitus* consist of a highly plastic and coevolved set of traits that include spawning periodicity, sites of egg deposition, mating behavior, fecundity, egg morphology, length of the breeding season, time of day when spawning occurs, and others, and that these traits are responses to differing selection pressures in local habitats. In *Menidia*, differences in predation pressure on adults and developing embryos seem to be associated with differences in reproductive behavior and timing of spawns in relation to the time of high tide, but other selective factors may be involved. Work in additional habitats is required and, more importantly, the genetic basis of variations in reproductive strategy between conspecific populations of fishes needs to be experimentally explored.

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