Copeia, 1981(4), pp. 766–776

Reproductive Ecology and Spawning Periodicity of the Atlantic Silverside, *Menidia menidia* (Pisces: Atherinidae)

DOUGLAS P. MIDDAUGH

The reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia*, was studied in the North Edisto River estuary, South Carolina, at Bears Bluff and the Point of Pines during the spring and summer, 1976–1978. Spawning runs occurred only in daytime and coincided precisely with the predicted time of high tide. Spawning by large numbers of fish in a small area at high tide, when tidal current and velocities were low, caused depletion of dissolved oxygen to <1.0 mg/l. *M. menidia* spawned in the upper intertidal zone at elevations of 1.2 to 2.4 m above mean low water.

Observed maxima in spawning-run index values occurred near the time of new and full moons, suggesting that the spawning population is synchronized by a lunar cue. The coincidence of a high tide at the time of sunrise every two weeks (high tide–sunrise cue) also may have served as a synchronizer for the spawning population. Determination of the relative importance of each factor was made difficult by their approximate synchrony during the March-July spawning season.

Many predators fed on spawning *M. menidia*. Several predators, including the ruddy turnstone, *Arenaria interpres morinella*, semipalmated sandpiper, *Ereunetes pusillus*, and blue crab, *Callinectes sapidus*, fed on developing *M. menidia* embryos.

Larval emergence was limited to times of tidal inundation. More larvae hatched during high tides at night than during the day.

THE Atlantic silverside, *Menidia menidia* (Linnaeus), is a small estuarine fish that ranges from the Magdalen Islands, Quebec, Canada (Cox, 1921) to Florida (Gosline, 1948; Robbins, 1969; Johnson, 1975). It is euryhaline and has been collected at salinities of 2.0‰ or less (De Sylva et al., 1962; Dahlberg, 1972), although Jerome et al. (1965, 1966) observed that it prefers salinities greater than 12‰. *M. menidia* is eurythermal and remains in Atlantic estuaries throughout most of the year (Kendall, 1902; Needler, 1940; De Sylva et al., 1962; Dahlberg, 1972).

Adults spawn from March through August, depending upon the latitude. Ripe fish were found in June at Prince Edward Island, Canada; during April in Chesapeake Bay (Leim and Scott, 1966; Nichols, 1908; Hildebrand and Schroeder, 1928; Bayliff, 1950); and along the coasts of North and South Carolina from March through August (Smith, 1907; Hildebrand, 1922; Middaugh and Lempesis, 1976). Spawning occurs in the upper intertidal zone, with females releasing up to 500 eggs, 0.9–1.2 mm in diameter. The eggs are attached to intertidal vegetation by a number of threads about five times as long as the diameter of the egg (Goode, 1884; Hildebrand, 1922; Bayliff, 1950). Developmental time of *M. menidia* embryos is temperature dependent; the incubation period ranging from 7 days as 21 C to 15 days at 18 C (Costello et al., 1957; Middaugh and Lempesis, 1976).

My preliminary field observations during 1973–1975 suggested that reproduction in *M. menidia* may be regulated by several factors, including lunar phase, tidal heights and a suitable substrate for spawning. My study examined the timing and intensity of spawning runs, intertidal distribution and survival of embryos, and time of larval emergence.

MATERIALS AND METHODS

Study sites.—Bears Bluff, Wadmalaw Island (32°38′42″ N, 80°15′18″ W) and the Point of Pines, Edisto Island (32°35′12″ N, 80°13′48″ W) are located on the North Edisto River estuary in South Carolina, U.S.A. Each site is characterized by an extensive intertidal mudflat progressing into a zone of cordgrass, *Spartina alterniflora,* and a narrow sandy beach in the upper intertidal zone. The estuary has high salinities with minimal runoff from land. The maximum spring tide range is approximately 2.5 m.

Three intertidal transects were established at Bears Bluff, beginning in the upper intertidal zone and extending down to an elevation below that at which *M. menidia* had been observed to spawn in previous years. The position of transects at Bears Bluff was based upon observations made from 1973 to 1975 on locations used most frequently for spawning. Two transects at the Point of Pines were established on the basis of observed spawning runs during the early part of this study. Stations, marked with a wooden stake, were positioned at 1–2 m intervals along each transect, depending on the slope of elevation.

Environmental measurements.—An immersion thermometer and refractometer were used to measure water temperature and salinity during spawning runs. Measurements were taken each day of a run at the beginning and end of the spawning season, March–June or July, and several times each week during other months if spawning runs occurred. A portable dissolved oxygen meter was used on several occasions to measure oxygen concentrations in areas where fish were spawning. Predicted tidal data for the March–July period of 1976–1978, computed for Bears Bluff by the National Ocean Survey, NOAA, were used in the analysis of spawning periodicity for both study sites.

Spawning periodicity.—In preliminary observations from 1973 through 1975, spawning runs were observed from early March through July during daytime high tides. Therefore, field observations were made from approximately 1 h before to 1 h after daytime high tides during March–July 1976 through 1978 at Bears Bluff. The Point of Pines was monitored during April–July of 1976 and March–July 1977 and 1978. If observations were not possible on a specific daytime high tide, careful checks for embryos were made on subsequent low tides. When embryos were found that could not be attributed to an observed spawn, the embryological stage was determined and the day of spawning estimated on the basis of developmental rates determined in the laboratory at temperatures similar to those observed in the field. Observations were also made during nighttime high tides for a continuous 30-day interval, beginning in March 1976 and again during April 1978. In addition, observations were made over entire tidal cycles several times during the three-year study. The purpose was to learn if spawning runs occurred at times other than daytime high tides and in locations other than the upper intertidal zone.

Since any movement by the observer within approximately 5 m of the spawning zone frightened spawners away on days with light spawning runs, a "Spawning-Run Index" with numerical values from 0 to 5 was developed and used to estimate the intensity of spawning runs, thereby avoiding the disturbance of quantitative seining (Table 1).

After developing criteria for assigning numerical values to a spawning run, Geoffrey I. Scott and I concurrently, but independently, observed several spawns at Bears Bluff and the Point of Pines during May and June 1976. In

TABLE 1. CRITERIA USED TO ASSIGN "SPAWNING-RUN INDEX" VALUES TO OBSERVED SPAWNS.

Values	Criteria
0	No spawning run observed or detected on subsequent low tides.
1	Very light spawning run; usually short duration, 5 to 40 min; no visible discoloration of water by milt from spawning males.
2	Light spawning run; usually short duration, 15 to 60 min; slight discoloration of water by milt confined to immediate shoreline.
3	Moderate spawning run; duration approximately 40 to 60 min; discoloration of water by milt extending to 0.5–1 m offshore and usually 5–10 m along the shore.
4	Heavy spawn; usually lasting from 40 to 60 min; discoloration of water by milt extending 1–3 m offshore and 10–15 m along shore; behavior of spawners indicates moderate depletion of dissolved oxygen in immediate area of the spawn; spent fish moving 10–15 m offshore and gasping at the surface.
5	Very heavy spawn; usually lasting for 40 to 60 min; discoloration of water by milt extending up to 5 m offshore and 15–20 m along shore; behavior of spawners indicates severe depletion of dissolved oxygen in immediate area of the spawn; spent fish moving 10–15 m offshore and gasping at the surface.

TABLE 2. SUMMARY OF PAIRED COMPARISON t-TESTS OF BEGINNING, MEDIAN AND END TIMES OF OBSERVED SPAWNS AND THE CONCURRENT PREDICTED TIME OF HIGH TIDE. BST = beginning spawn time, MST = median spawn time, EST = end spawn time and PTHT = predicted time of high tide. If concurrent spawning runs were observed at the two study sites, the earliest beginning time and latest end time of spawning were used to estimate the median spawn time. Clock times were converted to hours:tenths (i.e., 11:06 = 11:1 hours).

Variable	N	$\bar{x}$	$\bar{x}$ Diff.	S	t	P
BST		10:47				
PTHT	89	10:93	0.4607	0.0709	6.13	<0.0001
MST		10:85				
PTHT	87	10:90	0.0592	0.0634	0.80	>0.427
EST		11:06				
PTHT	92	10:71	−0.3511	0.0803	−4.20	<0.0001

most instances, our estimates of intensity were identical, and never varied by more than one "Spawning-Run Index" unit. G. I. Scott observed spawning and assigned "Spawning-Run Index" values at one site while I made similar observations at the other.

Beginning in May of 1976, spawning-run index values were assigned to each spawn immediately after it had occurred. Values based on field notes were assigned to spawning runs observed prior to development of the index (i.e., during March and April 1976). Spawns not observed, but detected on subsequent low tides, were assigned an intensity value based on the extent of egg deposition.

Embryo distribution and survival.—To determine intertidal distribution of developing embryos and their survival, we collected samples three to four days after a spawning run had occurred within one or more of the intertidal transects during 1976 and 1977. Replicate 0.125 m^2 samples were taken next to each stake that marked a transect station. Samples were preserved in 8% neutral-buffered formalin that contained a small amount of "Rose Bengal" dye. The dye colored the chorion and aided counting and classification of embryos as viable or nonviable, on the basis of eye pigmentation. Use of eye pigmentation as a criterion for viability did not allow an estimation of the percentage of embryos that would hatch, but did give an indication of embryo survival during the first three to four days of development.

Timing of larval emergence.—In a field experiment designed to study factors regulating the time of larval emergence, groups of embryos were removed from their locations within the intertidal zone six to nine days after fertilization. Parcels of 50 to 200 eyed embryos were placed in four 5-cm lengths of 1.5-cm I.D. glass tubing. A piece of 150-μm mesh plankton netting was stretched over each end of the tube. Four tubes were placed in the intertidal zone at the elevation of the embryos that had been sampled. Two tubes were removed 30 and 60 min after being inundated by the rising flood tide. Each set of two tubes and contents was preserved in 8% neutral-buffered formalin-seawater, and developing embryos and hatched larvae were counted.

RESULTS

Spawning periodicity.—Spawning runs of *M. menidia* occurred only during daytime, from 0700–1935 hours and coincided with the predicted time of high tide. Spawning took place only in the upper intertidal zone. Paired comparison t-test of mean differences showed that the beginning and ending of spawning runs bracketed and were significantly different from the predicted time of high tide, but the estimated median spawn time and the predicted time of high tide were not significantly different (Table 2). Observations for spawning runs were made on >90% of the days during the spawning season from 1976–1978. Mean daily spawning-run index values for observed or subsequently detected spawns were calculated. These values indicated an approximate fortnightly periodicity in occurrence of maximum intensity spawning runs by *M. menidia* from 1976 through 1978 (Figs. 1, 2, 3). Although it is obvious that maximum intensity spawning runs occurred at the approximate time of new and full moons at each study site, many low

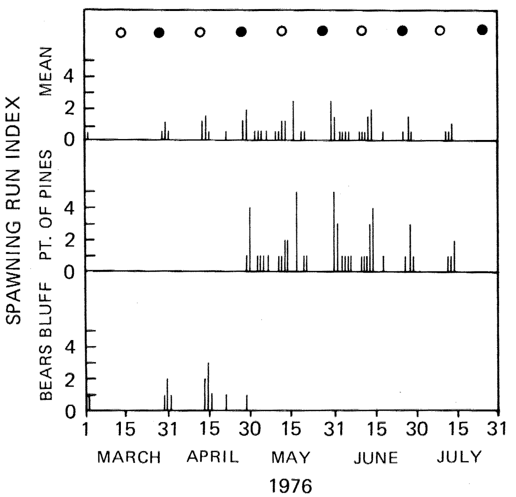

Fig. 1. Mean daily spawning-run indices for Bears Bluff and Point of Pines during 1976. Daily values for each study site are also shown. Filled circles = new moons; open circles = full moons.

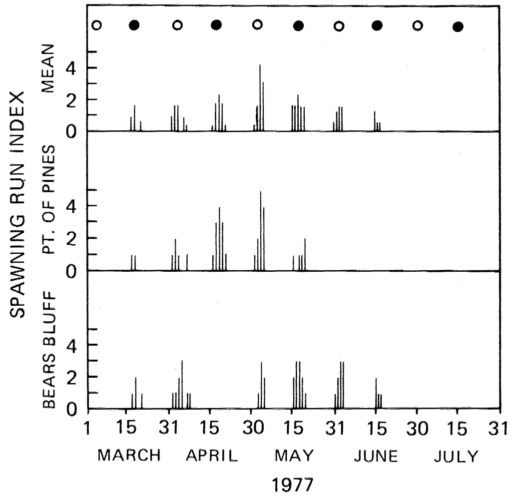

Fig. 2. Mean daily spawning-run indices for Bears Bluff and Point of Pines during 1977. Daily values for each study site are also shown. Filled circles = new moons; open circles = full moons.

intensity spawns were observed at other times. In addition, the frequency and intensity of runs at each site varied considerably during 1976–1978.

Correlation analyses were conducted to determine if spawning intensity and predicted high-tide heights were related. The mean daily spawning-run index values were compared with predicted heights of daytime high tides. No correlation was found between tidal heights and spawning-run index values ($r = -0.05$, $P > 0.1$).

Since spawning-run index values and predicted high-tide heights were not correlated, other factors were examined as potential cues for synchronization of spawning. Along the southeastern coast of the United States, the lunar semidiurnal partial tides (period 24.8 h) and solar semidiurnal partial tides (period 24.0 h) come into phase and summate every 14.77 days, at the time of the new and full moon, and cause spring tides twice in each synodic month (29.53 days). From March through July, phase synchrony of the lunar and solar semidiurnal tides also causes recurrence of high tides soon after sunrise on days immediately preceding the new and full moon. Since the lunar day of 24.8 h results in a 0.8 h delay in the time of high tide relative to the solar day of 24.0 h, the high tides occur successively later after sunrise through one semilunar cycle.

Night observations for spawning runs in March 1976 and in April and May 1978, while conducting larval emergence studies, showed that *M. menidia* were present in the upper intertidal zone on high tides, but did not school or spawn. Since spawning runs were not observed during nighttime high tides, apparently

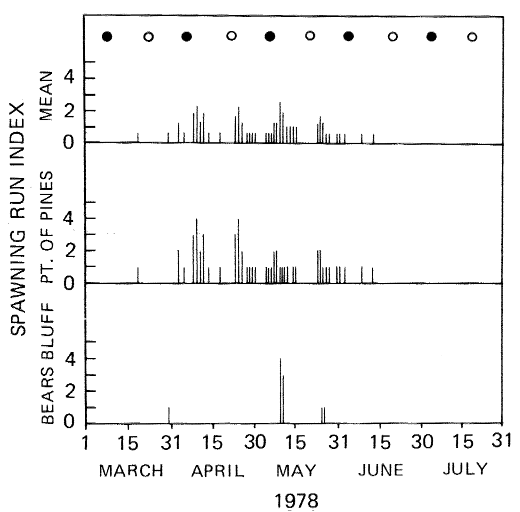

Fig. 3. Mean daily spawning-run indices for Bears Bluff and Point of Pines during 1978. Daily values for each study site are also shown. Filled circles = new moons; open circles = full moons.

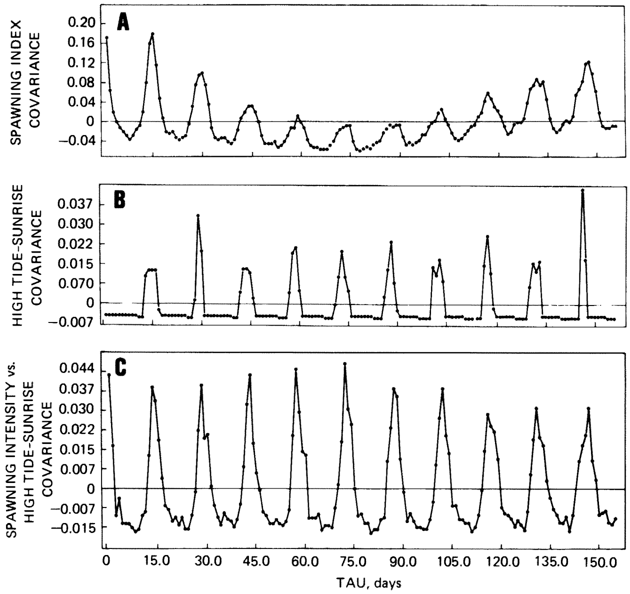

Fig. 4. A) Autocovariance function for mean daily spawning-run index values, and B) for the occurrence of a high tide immediately (<1 h) after the appearance of the upper limb of the sun above the horizon. C) Cross-covariance analysis of spawning cycles and occurrence of a high tide immediately after sunrise. In all cases, the mean period was 15 days. Yearly intervals of 156 days (late February–July) were analyzed for 1976–1978.

M. menidia can spawn only during daylight hours, especially if schooling is a behavioral prerequisite for spawning. Thus, the coincidence of a high tide and sunrise approximately every two weeks could serve as a synchronizer for spawning and cause approximately fortnightly peaks in the "Spawning-Run Index."

Time series analyses (Blackman and Tukey, 1958) were conducted to determine the periodicity of spawning runs and of the coincidence of high tides at sunrise. Procedures and assumptions used in coding data for autocovariance analyses were: 1) a mean spawning-run index value was assigned for each day that a spawning run (or runs) was observed; 2) if a spawn was detected by finding embryos in the intertidal zone, the day of spawning was estimated from the stage of development of the embryos; 3) on days when observations were not made and which could not be accounted for by subsequent observations at low tide, a value of 99999 (missing data) was assigned and all other days were assigned values of zero; 4) for analysis of the coincidence of high tide and sunrise, days on which high tide occurred immediately (<1 h) after the appearance of the upper limb of the sun above the horizon were assigned values of 1.0, all other days were assigned values of zero; and 5) for each of the three years, a 156-day interval was used. The BMD 02T-Autocovariance and Power Spectral Analysis Program (revised 24 December 1975, Health Sciences Computing Facility, Univ. of California, Los Angeles) was used for analyses.

Autocovariance analyses of spawning runs in *M. menidia* demonstrated peaks occurred every 13 to 16 days (Fig. 4A). The mean interval between spawning peaks was 15 days. Analysis of data for the coincidence of high tides occurring at sunrise also showed a periodicity of 13 to 16 days with a mean period of 15 days (Fig. 4B). Thus, it is possible that the high tide–sunrise cue could have served as a synchronizer for the observed spawning peaks.

Additional evidence for the potential importance of the high tide–sunrise cue comes from cross-covariance analysis of the spawn data and coincidence of high tide–sunrise data. Peaks occurred every 12 to 16 days; the mean period between peaks was 15 days (Fig. 4C). The tidal portion of the high tide–sunrise cue is linked by celestial mechanics to the recurrence of successive new and full moons which have an average period of 14.77 days. Therefore, it is dif-

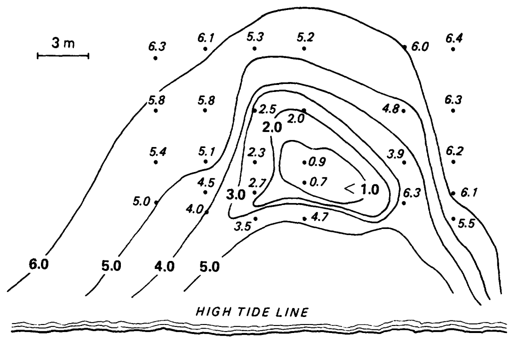

Fig. 5. Dissolved oxygen isopleths for a spawning run observed on 31 May 1976 at Point of Pines. Values are mg/l of dissolved oxygen measured 10 cm below the surface.

ficult to separate the influence of new and full moons and the nearly simultaneous occurrence of a high tide at sunrise as potential synchronizers for spawning.

During 1976, the first spawning run occurred at a water temperature of 16 C, and the occurrence of a new moon (2 March) nearly coincided. For 1977 and 1978, when first spawning was about 16 days later than in 1976, respective water temperatures were 18 C and 20 C. The delay in spawning in 1977 and 1978 may be related to attainment of a minimum water temperature necessary for spawning (16 C) and also to the time of occurrence of minimum temperature relative to time of a new or full moon, or to the coincidence of a high tide at sunrise. The spawning season ended in July 1976 and June of 1977 and 1978, when the water temperature was between 29 C and 30 C. Salinities measured during spawning runs ranged from 20–28‰ at Bears Bluff and 24–31‰ at the Point of Pines.

Oxygen depletion and predation.—When utilizing cordgrass as a spawning substrate, large numbers of *M. menidia* often spawned in a very limited area, ranging from 1 m^2 for low intensity spawning runs up to 10–15 m^2 for certain maximum-intensity spawning runs. Water depths ranged from 0–30 cm in the spawning zone. During the spawning run of 30 April 1976 at the Point of Pines, an apparent depletion of dissolved oxygen occurred in the spawning zone. Measurements made 10 cm below the water surface for a spawning run observed on 31 May 1976 revealed dissolved oxygen was reduced from an ambient concentration of 5–6 mg/l to <1.0 mg/l. The spawning run was very heavy (estimated spawning-run index = 5). Measurements were taken while the spawning run was in progress, about 30 min after it had begun. Greatest depletion of dissolved oxygen occurred in an area corresponding to the highest concentration of spawning fish (Fig. 5).

TABLE 3. PREDATORS OBSERVED TO FEED ON SPAWNING ADULTS OR DEVELOPING EMBRYOS OF *M. MENIDIA*. Asterisk denotes predators that consumed embryos in the intertidal zone.

INVERTEBRATES	
Blue crab*	*Callinectes sapidus*[1]
REPTILES	
Diamondback terrapin	*Malaclemys terrapin*
FISHES	
Spotted seatrout	*Cynoscion nebulosus*
Bluefish	*Pomatomus saltatrix*
Longnose garfish	*Lepisosteus osseus*
Atlantic stingray	*Dasyatis sabina*
Sandbar shark	*Carcharhinus plumbeus*
BIRDS	
Brown Pelican	*Pelecanus occidentalis carolinensis*
Common Egret	*Casmerodius album egretta*
Snowy Egret	*Leucophoyx thula thula*
Least Tern	*Sterna albifrons*
Common Tern	*Sterna hirundo hirundo*
Forster's Tern	*Sterna forsteri*
Laughing Gull	*Larus atricilla*
Cormorant	*Phalacrocorax auritus*
Black Skimmer	*Rhynchops nigra nigra*
Ruddy Turnstone*	*Arenaria interpres morinella*
Semipalmated Sandpiper*	*Ereunetes pusillus*

[1] Denotes predators that also consume adults.

Spotted seatrout, *Cynoscion nebulosis,* and bluefish, *Pomatomus saltatrix,* were often observed feeding on pre-spawning schools of *M. menidia,* but were excluded from the center of the spawning zone during the heavy spawning run of 31 May 1976. Small *P. saltatrix* penetrated no further than the 4 mg/l dissolved oxygen isopleth, whereas *C. nebulosis* moved inshore as far as the 2.5–3.0 mg/l isopleth. No predacious fish were observed in the area of most intense spawning and lowest dissolved oxygen.

Another behavioral phenomenon was noted during the intense spawning run of 31 May

TABLE 4. SUMMARY DATA FOR DEVELOPING EMBRYOS COLLECTED FROM INTERTIDAL TRANSECTS AT BEARS BLUFF AND THE POINT OF PINES.

Elev. class meters above MLW	Mean no. of embryos/0.125 m²		Mean % survival	
	Bears Bluff	Pt. of Pines	Bears Bluff	Pt. of Pines
1.01–1.20	0	0	—	—
1.21–1.40	0	3,167	—	19.1
1.41–1.60	10	2,091	12.1	44.5
1.61–1.80	236	5,010	36.9	13.5
1.81–2.00	1,027	2,516	27.7	63.1
2.01–2.20	2,014	0	6.7	—
2.21–2.40	96	0	20.0	—

1976. Spent fish that remained at the air-water interface swam to a position 10–15 m offshore from the spawning zone and formed a tightly grouped aggregation without schooling. The offshore aggregation was maintained while spawning continued inshore, but quickly disappeared from surface waters after a spawning run ended. During very heavy spawning runs, fish that formed nonschooling aggregations appeared to be stuporous and could be approached with ease. Low intensity spawns (spawning-run index = 1 or 2) did not produce the "stupor-like" effect.

Several species of fishes and birds fed on adult *M. menidia* during spawning runs and on developing embryos in the intertidal zone (Table 3). Evidence of the ability of developing *M. menidia* embryos to withstand stress was obtained by analysis of droppings left by ruddy turnstones, *Arenaria interpres morinella*, which were observed to feed on embryos in the upper intertidal zone at the Point of Pines. Two samples of droppings revealed a large number of imploded egg cases, as well as numerous embryos. Two intact embryos that had passed through the digestive tract were still alive.

Embryo distribution and survival.—Collections of embryos along each transect at Bears Bluff and the Point of Pines indicated that *M. menidia* spawns over a wide range of intertidal elevations. Pooled data for all Bears Bluff and Point of Pines transects are summarized in Table 4. Maximum numbers of embryos at Bears Bluff occurred at 2.01–2.20 m above mean low water (MLW). For the Point of Pines, maximum numbers of embryos occurred from 1.61–1.80 m above MLW. The greatest percentage of viable embryos, up to the time of collection, was 36.9% at 1.61–1.80 m above MLW at Bears Bluff and 63.1% at 1.81–2.00 m at the Point of Pines. There was no correlation between number of embryos collected from each intertidal elevation interval and percent survival of embryos ($r = -0.01$, $P > 0.47$).

Timing of larval emergence.—Embryos from a spawning run observed on 11 April 1978 at the Point of Pines were placed in glass tubes and monitored to determine the percentage emergence of larvae during successive flood-tide inundations beginning on 17 April. Larval emergence occurred primarily during nighttime high tides (Fig. 6). Tidal inundations on 17 and 18 April resulted in a low percentage of larval emergence. Much higher emergence, 70–75 percent for respective inundation periods of 30 and 60 min, was observed during nighttime inundations on 19 and 20 April.

DISCUSSION

Spawning periodicities have been described for a number of marine organisms. In many instances, the periodicity seems to be adjusted to provide maximum potential for survival of early life stages (Hefford, 1931; Korringa, 1957; Palmer, 1973; DeCoursey, 1976; McDowall, 1968; 1969). During the present study, spawning runs by *M. menidia* also seemed to be timed to increase the probability of reproductive success and survival of developing embryos.

Precise timing of spawning runs in *M. menidia* to coincide with the predicted time of high tide may increase the likelihood of egg fertilization. Sperm entering the water during an interval of diminished tidal currents would not be as susceptible to dispersion as during other times in the tidal cycle, when current velocities were higher. Moore (1980) observed a spawning run of *M. menidia* in a South Carolina estuary during ebb tide. Eggs were deposited in an algal mat on the downstream side of a floating dock, where the spawners were shielded from tidal currents.

In the present study, spawning at a time when current velocities were minimal resulted in depletion of dissolved oxygen during heavy spawning runs. The advantage, if any, of spawning in a confined area under conditions of severe oxygen depletion is not known. Perhaps the most plausible explanation is that low dissolved oxygen prevented intrusion of certain predacious fish, such as spotted seatrout, *Cynoscion nebulosus,* and bluefish, *Pomatomus saltatrix,* into the spawning zone.

Recently, Johannes (1978) pointed out that several schooling fishes are easily approached and captured while on the spawning grounds. These fish, he stated, seem to exhibit a kind of spawning stupor. In my study, during very heavy spawning runs, *M. menidia* also behaved as if in a spawning stupor, especially during the period immediately after spawning, when they formed nonschooling aggregations just offshore from the spawning zone. On the basis of observations with *M. menidia,* it seems possible that spawning stupor in other fishes could result from depressed dissolved oxygen concentrations on the spawning grounds.

In addition to precise timing of *M. menidia* runs with the predicted time of high tide, an approximate fortnightly periodicity in spawning-run index values was observed, maximum intensity generally occurring shortly after new and full moons. The slight, semidiurnal inequality in high tide heights in the North Edisto River estuary apparently was not a limiting factor for spawning *M. menidia,* as has been theorized for other atherinids including the California grunion, *L. tenuis,* and Gulf of California grunion, *L. sardina* (Walker, 1949, 1952; Thomson and Muench, 1976). Although semidiurnal inequality in tides did not seem to be an important factor, no spawning runs were observed during nighttime high tides. Schooling of *M. menidia* occurs by visual response between individuals. Shaw (1961) found that the critical light intensity for schooling of *M. menidia* was approximately 0.06 ft. candles; schools dispersed at lower light intensities. Therefore, spawning may be limited to daytime high tides, especially if schooling is a prerequisite for spawning. Since *M. menidia* spawning runs occurred precisely at the predicted time of daytime high tides, the cue for spawning may have resulted from decreased tidal current velocities at high tide.

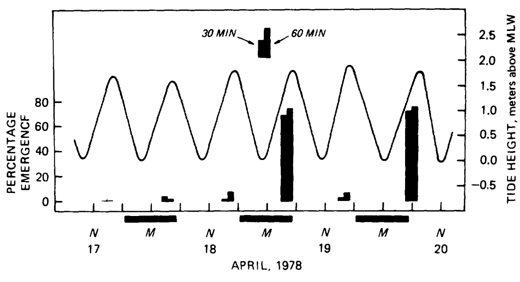

Fig. 6. Emergence of larval *M. menidia* during successive high tide inundations. Eggs were spawned on 11 April 1979 at Point of Pines; a trend of increased hatching during hours of darkness is evident. N = noon, M = midnight; hours of darkness are depicted by black bars.

The time from sunrise to the predicted time of high tide may have controlled the intensity of spawning runs. As the time between sunrise and predicted time of high tide increased, there would be a greater opportunity for fish that had dispersed during the nighttime to regroup into a school. Thus, size of the pre-spawning school may increase with the concurrent daily increase in time from sunrise to the predicted time of high tide. Daily increases in the number of fish schooling and spawning would eventually lead to a decline in spawning-run index values during respective fortnightly cycles, because a progressively larger number of individuals would be spent.

Intensity of daily spawning runs may also have been controlled by some density-dependent intragroup stimulant, related to the number of ripe *M. menidia* present in a school as the time of high tide approached. Such a mechanism has been suggested to explain initiation of spawning in the American smelt, *Osmerus mordax* (Rupp, 1965), and the surf smelt, *Hypomesus pretiosus* (Penttila, 1978). Carefully designed laboratory experiments in which diurnal and tidal cycles can be controlled and varied, relative to each other, may provide definitive information on the importance of the high tide–sunrise cue as a synchronizer for spawning in *M. menidia.*

During spawning, *M. menidia* used cordgrass, detrital mats or exposed cordgrass roots in abandoned crab burrows as a spawning substrate. Threads that appeared on hydrated *M. menidia* eggs, immediately after they were spawned, helped to anchor the developing embryos at the intertidal elevation where spawning occurred. Intertidal distribution of embryos demonstrated that they were deposited at elevations ranging from 1.20–2.40 m above MLW. The elevation of egg deposition by the California grunion, *L. tenuis,* was examined by Thompson and Thompson (1919) at La Jolla, California. Most eggs were located at approximately 1.6 m above MLW, which compares favorably with the occurrence of *M. menidia* embryos within the intertidal zone. The maximum tidal height at La Jolla, approximately 2.1 m, is similar to the 2.5 m tidal range in the North Edisto River estuary.

Recently, Taylor et al. (1977, 1979) observed that the mummichog, *Fundulus heteroclitus,* exhibited a lunar spawning periodicity and deposited eggs on the inner surfaces of primary leaves of cordgrass, *Spartina alterniflora,* apparently during nighttime high tides. Developing embryos were located at an elevation of 0.85–0.90 m above MLW in an area with tidal fluctuations of 1.0–1.5 m. Thus, intertidally spawned eggs of *M. menidia* and *F. heteroclitus,* deposited on relatively stable substrates in low energy environments, are usually inundated by high tides on a daily basis.

In contrast, *L. tenuis* spawns on high energy beaches of southern California, depositing eggs in an unstable sand substrate. Spawning occurs during nighttime high tides, generally on a decreasing tide series, when subsequent high tides are of lower amplitude, thus helping to prevent uncovering of embryos prior to completion of development (Shepard and LaFond, 1940). However, the eggs may not be moistened by tidal inundation for several weeks or longer (Walker, 1949).

Only three predators, the blue crab, *Callinectes sapidus,* ruddy turnstone, *Arenaria interpres morinella,* and semipalmated sandpiper, *Ereunetes pusillus,* were observed to feed on developing *M. menidia* embryos. Blue crabs were detected foraging on embryos at Bears Bluff and the Point of Pines several times during high tides. Ruddy turnstones and semipalmated sandpipers were observed feeding on embryos only at the Point of Pines. Passage of viable embryos through the digestive tract of ruddy turnstones is good evidence of the integrity of the chorion protecting *M. menidia* embryos. Thompson and Thompson (1919) found that a histerid beetle, *Sparinus salcifrons,* was the only serious predator of *L. tenuis* embryos. Walker (1949) reported that shorebirds, including marbled godwits, *Limosa fedosa,* and Hudsonian curlews, *Numenius phaepus hudsonicus,* actively probed the sand in search of *L. tenuis* embryos. Western gulls, *Larus californicus,* were observed feeding on embryos left at the surface by godwits and curlews.

Larval emergence seems to be timed to increase the likelihood of survival. Since *M. menidia* eggs are deposited in the upper intertidal zone, time of hatching depends on flood tide inundation. A diurnal rhythm that partially inhibits hatching during daytime high tides appears to be present. One obvious benefit of larval emergence at night would be a decreased opportunity for predation during the first few hours after emergence. Kendall (1902) reported that *M. menidia* is an opportunistic omnivore and will eat its own eggs and larvae.

In summary, results of this study indicate that the reproductive ecology of the Atlantic silverside, *M. menidia,* is closely coordinated with periodically recurring environmental factors. Spawning runs occurred only during daylight hours precisely at the predicted time of high tide. Dissolved oxygen concentrations decreased in the spawning zone during heavy spawning runs. Maxima in spawning-run index values were observed at the approximate time of the new and full moons. The high tide–sunrise cue which occurs at the approximate time of new and full moons may synchronize spawning.

Eggs were deposited at the base of cordgrass plants, in detrital mats, or in abandoned crab burrows at elevations of 1.2–2.4 m above MLW. Larval emergence occurred during tidal inundations, with maximum emergence on nighttime high tides.

Acknowledgments

The author is indebted to G. I. Scott for approximately 1,500 hours of field observations. A. C. Badger, G. Floyd, P. W. Lempesis and C. McMillan also provided assistance in conducting field observations. R. G. Domey and G. W. Schreyer performed statistical analyses. I also thank R. E. Johannes, R. M. McDowall and B. W. Walker for their helpful criticisms of the manuscript.

Contribution 400 of the Gulf Breeze Environmental Research Laboratory. Contribution 355 of the Belle W. Baruch Institute for Marine Biology and Coastal Research.

LITERATURE CITED

BAYLIFF, W. H. 1950. The life history of the silverside *Menidia menidia* (Linnaeus). Publ. Chesapeake Biol. Lab. 90:1–27.

BLACKMAN, R., AND J. TUKEY. 1958. The measurement of power spectra. Dover Publications, New York, N.Y.

COX, P. 1921. List of the fishes collected in 1917 off Cape Breton coast and the Magdalen Islands. Contrib. Canadian Biol., 1918–1920, 11:109–114.

COSTELLO, D. P., M. E. DAVIDSON AND A. EGGERS. 1957. Methods for obtaining and handling marine eggs and embryos. Marine Biological Laboratory, Woods Hole, Massachusetts.

DAHLBERG, M. D. 1972. An ecological study of Georgia coastal fishes. U.S. Fish Wildl. Serv. Fish. Bull. 70:323–353.

DECOURSEY, P. J. 1976. Biological rhythms in the marine environment. University of South Carolina Press, Columbia.

DE SYLVA, D. P., F. A. KALBER, JR. AND C. N. SCHUSTER. 1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary, with notes on other species collected in deeper water. Univ. Del. Mar. Labs., Information Ser., Publ. 5.

GOODE, G. B. 1884. The fisheries and fishery industries of the United States. Section 1: Natural history of useful aquatic animals: 448–467.

GOSLINE, W. A. 1948. Speciation in the fishes of the genus *Menidia*. Evolution 2:306–313.

HEFFORD, A. E. 1931. Report on fisheries for the year ended 31 March 1931. Rep. Fish. N.Z. 14:16–17.

HILDEBRAND, S. F. 1922. Notes on habits and development of eggs and larvae of the silversides *Menidia menidia* and *Menidia beryllina*. Bull. U.S. Bur. Fish. 38:113–120.

———, AND W. C. SCHROEDER. 1928. Fisheries of Chesapeake Bay. *Ibid.* 43:1–336.

JEROME, W. C., JR., A. P. CHESMORE AND C. O. ANDERSON, JR. 1966. A study of the marine resources of Quincy Bay. Mass. Div. Mar. Fisheries, Monograph Series 2.

———, ———, ——— AND F. GRICE. 1965. A study of the marine resources of the Merrimack River Estuary. *Ibid.* 1.

JOHANNES, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish 3:65–84.

JOHNSON, M. S. 1975. Biochemical systematics of the atherinid genus *Menidia*. Copeia 1975:662–691.

KENDALL, W. C. 1902. Notes on the silversides of the genus *Menidia* of the east coast of the United States, with descriptions of two new subspecies. Rep. U.S. Comm. Fish and Fisheries for 1901:241–267.

KORRINGA, P. 1957. Lunar periodicity. Geol. Soc. Amer. Memoir 67:917–934.

LEIM, A. H., AND W. B. SCOTT. 1966. Fishes of the Atlantic coast of Canada. Fish. Res. Bd. Canada, Bull. 155.

MCDOWALL, R. M. 1968. *Galaxias maculatus* (Jenyns), the New Zealand whitebait. N.Z. Mar. Dept. Fish. Res. Bull. 2(New Series):1–84.

———. 1969. Lunar rhythms in aquatic animals, a general review. Tuatara 17:133–144.

MIDDAUGH, D. P., AND P. W. LEMPESIS. 1976. Laboratory spawning and rearing of a marine fish, the silverside *Menidia menidia menidia*. Mar. Biol. 35:295–300.

MOORE, C. J. 1980. Spawning of *Menidia menidia* (Pisces: Atherinidae). Copeia 1980:886–887.

NEEDLER, A. W. H. 1940. A preliminary list of fishes of Malpeque Bay. Proc. Nova Scotian Inst. Sci. 20:33–41.

NICHOLS, J. R. 1908. A note on the silverside. Amer. Nat. 42:731.

PALMER, J. D. 1973. Tidal rhythms: the clock control of the rhythmic physiology of marine organisms. Biol. Rev. 48:377–418.

PENTTILA, D. 1978. Studies of the surf smelt (*Hypomesus pretiosus*) in Puget Sound. State of Washington, Dept. Fish., Tech. Rept. 42.

ROBBINS, T. W. 1969. A systematic study of the silversides *Membras* Bonaparte and *Menidia* (Linnaeus) (Atherinidae, Teleostei). Unpubl. Ph.D. Diss., Cornell Univ.

RUPP, R. S. 1965. Shore-spawning and survival of eggs of the American smelt. Trans. Amer. Fish. Soc. 94:160–168.

SHAW, E. 1961. Minimal light intensity and the dispersal of schooling fish. Bull. Inst. Oceanogr. Monaco 1213:1–8.

SHEPARD, F. P., AND E. C. LAFOND. 1940. Sand movements along the Scripps Institution pier. Amer. Jour. Sci. 238:272–285.

SMITH, H. M. 1907. The fishes of North Carolina. N.C. Geol. and Econ. Surv. 2:1–453.

TAYLOR, M. H., L. DIMICHELE AND G. J. LEACH. 1977. Egg stranding in the life cycle of the mummichog, *Fundulus heteroclitus*. Copeia 1977:397–399.

———, G. J. LEACH, L. DIMICHELE, W. M. LEVITAN AND W. F. JACOB. 1979. Lunar spawning cycle in the mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). Copeia 1979:291–297.

THOMPSON, W. F., AND J. B. THOMPSON. 1919. The spawning of the grunion. Calif. Fish and Game Comm. Bull., 3:1–29.

THOMSON, D. A., AND K. A. MUENCH. 1976. Influence of tides and waves on the spawning behavior of the Gulf of California grunion, *Leuresthes sardina*

(Jenkins and Evermann). Southern Calif. Acad. Sci. Bull. 75:198–203.

Walker, B. W. 1949. Periodicity of spawning by the grunion, *Leuresthes tenuis*, an Atherine fish. Unpubl. Ph.D. Diss. University of Calif., Los Angeles.

———. 1952. A guide to the grunion. Calif. Fish and Game 38:409–420.

Douglas P. Middaugh, Gulf Breeze Environmental Research Laboratory, Sabine Island, Gulf Breeze, Florida 32561. Accepted 23 Aug. 1980.

Copeia, 1981(4), pp. 776–784

Rearing of Embryos and Larvae of the Australian Lungfish, *Neoceratodus forsteri*, under Laboratory Conditions

A. Kemp

Larval lungfish were reared under laboratory conditions to stage 55 (52 mm). Suitable foods were daphnia, chironomid larvae and tubifex for all stages, and hen's egg yolk with or without vegetable juices for older stages. Increase in size of larvae was not affected by available space under the conditions of culturing described. Temperatures within the range of 18–22 C gave the same growth rate but 10 or 30 C were lethal to cleaving eggs. The conditions described permit rearing of lungfish for detailed embryological and histological studies.

The Australian lungfish, *Neoceratodus forsteri* Krefft from southeast Queensland is interesting because it is a primitive fish which has survived unchanged in Australia for millions of years. Also the embryological development is very similar to that of some urodele amphibians (Semon, 1893; Kemp, 1977). However, eggs and larvae are difficult to rear under laboratory conditions.

Early workers found that while it was easy to keep larvae alive for about 10 weeks after hatching, many died after this time (Semon, 1893, 1899; Bancroft, 1914). Illidge (1894) was able to rear larvae for 8 months, but Bancroft achieved better results, keeping young fish alive for several years by various methods. He used a separate container for each egg (Bancroft, 1914; 1918). The eggs and larvae lay in shallow water with a sloping sandy bottom and the fish were given larger containers as they grew (Bancroft, 1928). He gives no figures on larval mortality in these experiments but states that "very few survived" (1918:92). The last method described, making use of a circulating water system (Bancroft, 1933), apparently decreased mortality but again no figures were given.

The method used in this laboratory is based on Bancroft's earlier work but does not require elaborate equipment or circulating water. Large numbers of healthy fish can be produced for embryological and histological studies. Records of each specimen can be kept throughout development and the method can easily be adapted for experimental trials on individual fish.

Materials and Methods

Eggs of *N. forsteri* were collected from Enoggera Reservoir and from the Brisbane River, Queensland. Each egg was reared in an individual container of sterile tap water with the