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Reproductive Rhythmicity of the Atlantic Silverside

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Abstract

The reproductive periodicity of the Atlantic silverside *Menidia menidia* was studied at two locations on the North Edisto River estuary in South Carolina during March–July 1976–1978. Spawning runs occurred in the upper intertidal zone and coincided precisely with daytime high tides. Time-series analysis of daily changes in the intensity of spawning runs revealed a fortnightly reproductive periodicity and indicated that the observed reproductive rhythmicity in Atlantic silversides may be mediated by a high-tide–sunrise cue that also occurs at fortnightly intervals. During the 1976 and 1977 reproductive seasons, there were highly significant correlations ($P < 0.01$) among the male gonadal index, the female gonadal index, and the occurrence of intermediate, maturing, and hydrated-egg stages of sexual development in females. The percentage of females with hydrated eggs was greatest on days when a high tide occurred within 1 hour after sunrise.

The Atlantic silverside *Menidia menidia* resides in estuaries from the Magdalen Islands, Quebec, to northern Florida (Cox 1921; Robbins 1969). The species is euryhaline, occurring at salinities of 2–30‰ (DeSylva et al. 1962; Middaugh and Lempesis 1976). It is also eurythermal, remaining in many southern estuaries or the adjacent coastal surf zone throughout most of the year (Dahlberg 1972; Anderson et al. 1977; Shenker and Dean 1979). Populations from the Chesapeake Bay northward occur infrequently in, or are absent from, estuaries during midwinter. Conover and Murawski (1982) documented an offshore migration of Atlantic silversides north of Cape Hatteras in winter, generally to waters less than 50 m deep.

Recent evidence has shown that Atlantic silversides from estuaries at southern and northern latitudes are cyclical spawners, reproducing with a fortnightly periodicity (Middaugh 1981; Conover and Kynard, in press). At southern latitudes, the reproductive season extends from March through August (Hildebrand 1922; Middaugh and Lempesis 1976). Breeding takes place from April or May to July at northern latitudes (Bigelow and Schroeder 1953; Conover and Ross 1982).

This paper briefly reviews aspects of the reproductive rhythmicity in Atlantic silversides from the North Edisto River estuary in South Carolina (Middaugh 1981; Middaugh et al. 1981) and presents new data on (1) the simultaneous occurrence of several egg stages in females, (2) the gonadosomatic indices for adults during the 1976 and 1977 reproductive seasons, and (3) the relationship between appearance of hydrated eggs and the timing of high tides within 1 hour after sunrise every 2 weeks.

Methods

The study sites, Bears Bluff, Wadmalaw Island, and the Point of Pines, Edisto Island, are located on the North Edisto River estuary in South Carolina. A detailed description of the study sites and characteristics of the high-salinity estuary was provided by Middaugh (1981) and Middaugh et al. (1981).

TABLE 1.—*Criteria used to assign "spawning-run index" values to Atlantic silverside runs (after Middaugh 1981).*

Value	Criteria
0	No spawning run observed or detected on subsequent low tides.
1	Very light run; duration 5 to 40 minutes; no visible discoloration of water by milt from males.
2	Light run; duration 15 to 60 minutes; slight discoloration of water by milt.
3	Moderate run; duration 40 to 60 minutes; discoloration by milt extending 0.5–1 m offshore and 5–10 m along the shoreline.
4	Heavy spawn; duration 40 to 60 minutes; discoloration by milt 1–3 m offshore and 10–15 m along the shoreline.
5	Very heavy spawn; duration 40 to 60 minutes; discoloration by milt extending up to 5 m offshore and 10–15 m along the shoreline.

Spawning Periodicity

Observations were made from 1 hour before, until 1 hour after daytime high tides during March–July of 1976 through 1978 at Bears Bluff. The Point of Pines was monitored during April–July of 1976 and March–July of 1977 and 1978. Observations also were made during approximately 60 nighttime high tides to determine if spawning occurred during darkness.

Seining was not used to quantify the intensity of runs because it was believed that an individual probably spawned several times during the season. Thus, removal of fish from the populations at respective study sites during a given spawning run might have biased observations of subsequent runs. Moreover, on days with light spawning runs, we learned that movements by the observer within about 5 m of the spawning zone would disturb or interrupt reproductive activity. Therefore, we developed an observational "spawning-run index" with numerical values from 0 to 5 and used it to estimate the intensity of spawning runs (Table 1).

After observing several spawning runs as a group, we were able to make independent estimates of a spawning-run index value that did not differ by more than one unit. Thereafter, the first author monitored the Point of Pines and the third author the Bears Bluff study site.

Gonadosomatic Indices

Adults were collected at 2- to 5-day intervals from February through July of 1976 and 1977 to determine if changes occurred in gonadosomatic indices (100 × gonad weight/total body weight) during the reproductive season. A 1.5-m × 1.5-m × 1.0-m-deep drop net with 5-mm mesh, baited with hickory shad *Alosa mediocris,* was used to make collections from a pier adjacent to the Bears Bluff study site. In general, collections were made during an interval from 1 hour before until 1 hour after low tide. If less than 50 individuals were collected, all were analyzed. If more than 50 were captured, a sample of 50 was randomly selected for examination. The standard length (SL), wet weight (after gentle blotting), sex, and gonad weight of each individual was determined. From visual and microscopic examination, eggs in the ovaries of each female were categorized into four classes. A classification scheme similar to that employed by Clark (1925) for characterizing the maturing egg stages present in the cyclic (fortnightly) spawning California grunion *Leuresthes tenuis* was used (Table 2).

TABLE 2.—*Four egg stages present in Atlantic silversides.*

Stage	Egg diameter (D, mm)	Egg appearance
Immature	$D \leq 0.36$	Opaque white
Intermediate	$0.36 < D \leq 0.82$	Opaque yellow white
Maturing	$0.82 < D \leq 1.00$	Translucent amber
Hydrated	$D > 1.00$	Translucent amber with or without threads

Statistical Analyses

Observational data on the timing and intensity of spawning runs and concurrent environmental variables were examined by several statistical procedures. Analyses were based upon predicted times and heights of high tides computed for the Bears Bluff site by the National Ocean Survey, National Oceanographic and Atmospheric Administration. Predicted times of sunrise and sunset for Bears Bluff (32°38′45″N, 80°15′25″W) were extrapolated from *Astronomical Phenomena* issued by the Nautical Almanac Office, United States Naval Observatory.

We compared reproductive periodicity of Atlantic silversides and the period between successive occurrences of a high tide at sunrise (within 1 hour after appearance of the upper limb of the sun above the horizon) with the BMD 02T-Auto Covariance and Power Spectral Analysis Program (revised 24 December

1975, Health Sciences Computing Faculty, University of California, Los Angeles). Details of procedures for coding data were provided by Middaugh (1981).

Intercorrelation analyses were performed to measure the intensity of the relationship between the daily mean male gonadosomatic index (MGI), the concurrent female gonadosomatic index (FGI), and the occurrence of four egg stages within the ovaries. Stepwise inductive multiple-regression analyses of the gonad data were conducted in two parts. First, prediction of the MGI (dependent variable) as a function of the FGI and occurrence of intermediate, maturing, and hydrated eggs (independent variables) was examined. Additional analysis of the FGI (dependent variable) as a function of the occurrence of intermediate, maturing, and hydrated egg stages (independent variables) was also conducted. A chi-square test was performed to test the extrinsic hypothesis that dates of maximum frequency of females with hydrated eggs were not significantly different from corresponding days with a high tide within 1 hour after sunrise.

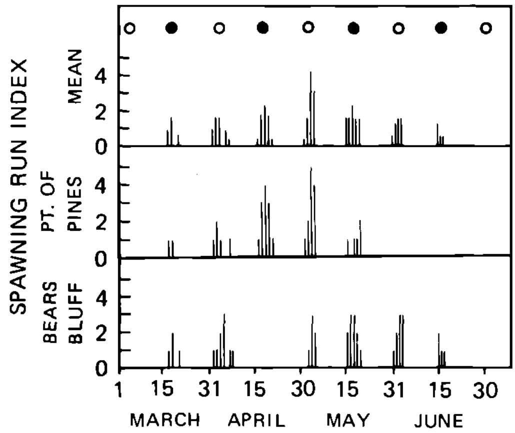

FIGURE 1.—*Daily spawning-run indices for Atlantic silversides at Bears Bluff and the Point of Pines during 1977 and the means of locality values. Filled circles = new moons; open circles = full moons. From Middaugh (1981).*

Results

Spawning Periodicity

Atlantic silversides spawned only during daytime. Runs coincided with the predicted time of high tide. The median spawn time and predicted time of high tide were not significantly different ($N = 87$; $t = 0.80$; $P > 0.43$). Spawning-run indices for 1977 indicated an approximate fortnightly periodicity for maximum-intensity runs, which occurred near the time of new and full moons (Fig. 1). Similar results were obtained during 1976 and 1978.

Although spawning runs of Atlantic silversides coincided precisely with the predicted time of high tides during daytime there was no correlation between the intensity of runs and the height of tides during spawning ($N = 234$; $r = 0.05$; $P > 0.1$. We searched for other potential environmental cues besides tidal height to explain the fortnightly spawning periodicity. In 1976 and 1978, we learned that Atlantic silversides were present in the upper intertidal zone on nighttime high tides, but did not school or spawn, even though intertidal substrates used for egg deposition were inundated. We also observed that daytime spawning runs always were preceded by the appearance of schooling Atlantic silversides offshore of the intertidal areas where eggs were deposited (Middaugh et al. 1981). Thus we inferred that schooling could be a behavioral prerequisite for spawning. Shaw (1961) observed that the critical light intensity for schooling of Atlantic silversides was approximately 0.7 lux; individuals dispersed at lower light intensities.

It seemed possible, then, that the coincidence of a high tide at sunrise (high-tide–sunrise cue) might both stimulate schooling and synchronize spawning with high tide, causing the approximate fortnightly peaks in spawning intensity (Middaugh 1981).

Time-series analyses were conducted to determine the periodicity of spawning runs; and of the coincidence of high tides at sunrise. Autocovariance analyses showed spawning-run peaks at 13- to 16-day intervals; the mean period was 15 days (Fig. 2). The same mean periodicity—15 days—resulted for high tides at sunrise and for cross-covariance of spawning runs and high tides at sunrise.

Gonadosomatic Indices

Gonadosomatic index (GSI) measurements for males and females showed an apparent trend of simultaneous increases then decreases that seemed to be related to observed maxima in spawning-run indices (Fig. 3 for 1977 data; 1976

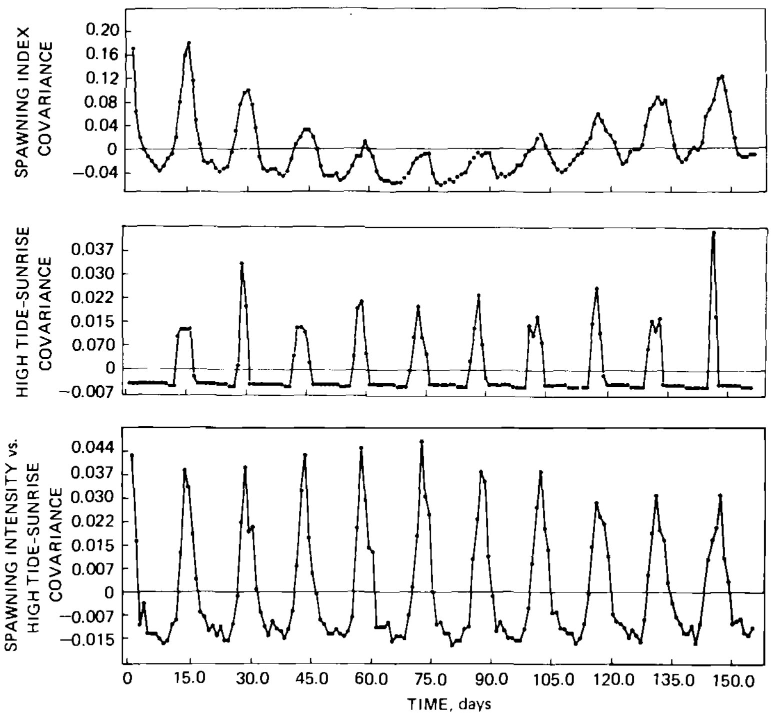

FIGURE 2.—*Autocovariance functions for mean daily spawning-run indices for Atlantic silversides, occurrences of high tide at sunrise, and the interaction of these variables. From Middaugh (1981).*

results are similar). Collections were made at various times (0730–1900 hours) during daylight; because Hubbs (1976) documented substantial changes in the GSI of inland silversides *Menidia beryllina* (originally reported as *M. audens*) collected at different times of day (and night), we believed it would not be appropriate to make direct comparisons of the GSI and daily spawning-run indices. However, all fish collected on respective days were captured simultaneously, so we were able to compare the GSI for males and females, and the percentage occurrence (among females) of immature, intermediate, maturing, and hydrated eggs. Male and female GSIs were highly correlated with each other and with the occurrences of several egg stages (Table 3).

Stepwise inductive multiple-regression analyses revealed that female GSI was the best predictor of male GSI, explaining 44% of its vari-

TABLE 3.—*Correlation* (r) *matrix for 98 comparisons of reproductive characteristics of Atlantic silversides, 1976, 1977. Asterisks indicate* $^{**}P < 0.01$. *Dashes indicate* r *could not be calculated. Gonadosomatic index is 100(gonad weight/body weight).*

	Gonadosomatic index		Frequency of egg-stage occurrence			
Variable	Males MGI	Females FGI	Immature IMM	Intermediate INT	Maturing MAT	Hydrated HYD
FGI	0.666**					
IMM	—	—				
INT	0.404**	0.363**	—			
MAT	0.440**	0.725**	—	0.276**		
HYD	0.313**	0.717**	—	0.150	0.662**	

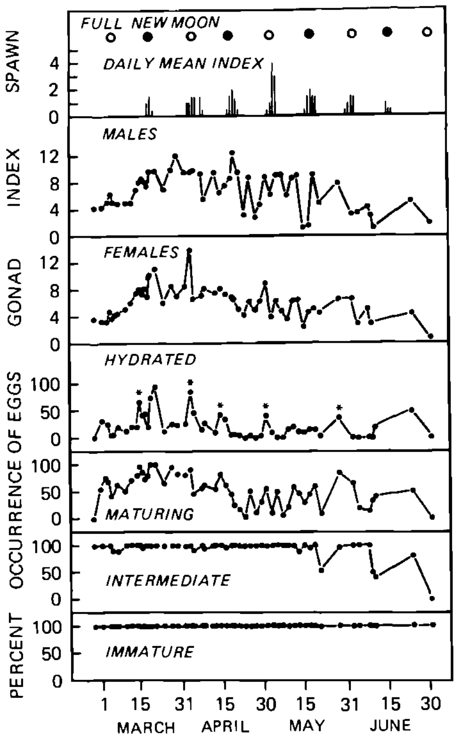

FIGURE 3.—*Spawning intensities, gonadosomatic indices, and frequencies of egg development stages for Atlantic silversides, 1977. The gonadosomatic index is 100 × gonad weight/body weight. Asterisks (*) indicate peak occurrences of hydrated eggs.*

ation (R^2, Table 4). The hydrated and intermediate egg stages accounted for only 7% more covariance, and the maturing eggs (not shown in Table 4) did not improve the regression at all. The female GSI was best predicted by the occurrence of mature eggs ($R^2 = 52\%$); hydrated and intermediate eggs explained an additional 14% of the variance (Table 4).

To determine if the high-tide–sunrise cue could play a role in synchronization of egg hydration and subsequent spawning, we performed the following analysis of data in Fig. 3. Dates of "peak" hydration (asterisks) were paired with respective dates for the subsequent new or full moon. Then the number of days between peak hydration and the subsequent new or full moon (observed) was compared to the number of days from the occurrence of a high tide within 1 hour after sunrise and the date of the subsequent new or full moon (expected). Inclement weather with heavy rain, high waves, and turbidity on March 20–21, 1977, apparently interrupted normal spawning patterns, thus resulting in the very high peak in females with hydrated eggs on March 21 (Fig. 3). This peak was not included in our analysis. There was no significant difference ($P > 0.10$) in observed and expected values (Table 5), and it appears that the occurrence of a high tide within 1 hour after sunrise may serve as an effective cue for egg hydration.

Discussion

Coincidence of spawning by Atlantic silversides with high tide minimizes the dispersion of sperm by water currents. Water velocities also are low at low tide, but appropriate spawning substrates for the species are unavailable then (Middaugh et al. 1981). As determined by Middaugh and Takita (1983), current velocities ranged from 3 to 16 cm·second^{-1} (mean = 11 cm·second^{-1}) at the onset of spawning. Runs ended when ebb-tide currents ranged from 5 to 22 cm·second^{-1} (mean = 17 cm·second^{-1}).

TABLE 4.—*Stepwise inductive multiple-regression prediction of male (MGI; N = 1,790) and female (FGI; N = 2,274) gonadosomatic indices by other reproductive characteristics of Atlantic silversides, including frequencies of occurrences of hydrated (HYD), mature (MAT), and intermediate-stage (INT) eggs. Asterisks denote **P < 0.01.*

Independent variables	R	Adjusted R	R^2	Pearson product-moment coefficient
		Dependent variable: MGI		
FGI	0.666**		0.444	0.666**
FGI + HYD	0.707**	0.699**	0.500	0.320**
FGI + HYD + INT	0.720**	0.709**	0.518	0.404**
		Dependent variable: FGI		
MAT	0.724**		0.521	0.724**
MAT + HYD	0.821**	0.817**	0.674	0.717**
MAT + HYD + INT	0.876**	0.872**	0.767	0.362**

TABLE 5.—*Observed date (1977) of "peak" hydration of Atlantic silverside eggs prior to respective new and full moons compared to expected date of hydration, expectation being based on the assumption that the occurrence of a high tide within 1 hour of sunrise serves as a cue for hydration. Chi-square = 1.12; df = 1; P > 0.1.*

Date of new or full moon	Date of hydration	Hydration-days before new or full moon (observed)	High tide–sunrise coincidence, days before new or full moon (expected)
Mar 19	Mar 15	4	3
Apr 4	Apr 3	1	3
Apr 18	Apr 14	4	4
May 3	May 1	2	3
Jun 1	May 28	4	4

Observations of spawning runs of Atlantic silversides from Salem Harbor, Massachusetts, revealed that daily spawning activity generally occurred shortly after high tide, as the water level began to recede (Conover and Kynard 1984). Timing of spawning runs by Atlantic silversides to coincide with the occurrence of very shallow water over suitable substrates would reduce the unit volume water per unit surface area of suitable substrate, thus increasing the concentration of milt on the spawning grounds. Middaugh et al. (1981) observed that Atlantic silversides from the North Edisto River estuary in South Carolina always spawned in very shallow water (<20 cm deep), precisely at high tide. Similar reproductive behavior was reported for other populations in Atlantic coast estuaries (Goode 1884; Hildebrand 1922; Bayliff 1950).

In this study significant correlations among the female and male GSI and occurrence of intermediate (INT), maturing (MAT), and hydrated (HYD) egg stages are indicative of a highly synchronized spawning population of Atlantic silversides. The occurrence of up to four stages of developing eggs within the ovaries and the observed reproductive rhythm suggests that sequential maturation takes place with an approximate fortnightly periodicity. As hydrated eggs move into the lumen and are spawned, maturing eggs then are available to enter the hydrated stage, while eggs in the intermediate class continue development to the maturing stage. The highest percentage of females with hydrated eggs occurred 1–4 days prior to the observed maxima in spawning-run indices. Moreover, the dates of peak egg hydration and the occurrence of a high tide within 1 hour after sunrise were nearly identical (Fig. 3; Table 5). This relationship suggests that physical factors serve as an important synchronizer for egg maturation.

Thus, the fortnightly lunar reproductive periodicity in Atlantic silversides, superimposed on the tidally influenced daily spawning periodicity, may be mediated by the coincidence of high tides (decreased current velocities) at the time of sunrise, which occurs about every 2 weeks during the spawning season.

Clark (1925) demonstrated that eggs within the ovaries of the California grunion also show periodic maturation. Rapid growth of ova occurred between the intermediate and mature (hydrated) class just prior to spawning near the time of new and full moons. A similar trend was noted by Taylor and DiMichele (1980) in the ovaries of sexually active semi-lunar spawning mummichogs *Fundulus heteroclitus*. Fish examined just prior to or during spawning activity contained a significantly greater proportion of mature eggs than at other times.

Physical stimuli are known to play an important part as proximate factors acting upon the endocrine-controlled gonadal cycles in fishes. These physical factors ensure that fish are ready to spawn at a time and location most favorable for survival of eggs and young (Liley 1969). It is likely that regularly recurring environmental variables serve as signals for a general synchronization of endogenous endocrine-controlled cycles of gonad maturation in intertidal fishes. They also may provide the final stimulus for synchronization of reproductive activity at a given time and location in the environment.

References

ANDERSON, W. D., J. K. DIAS, R. K. DIAS, D. M. CUPKA, AND N. A. CHAMBERLAIN. 1977. The macrofauna of the surf zone of Folly Beach, South Carolina. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) SSRF (Special Scientific Report Fisheries) 704.

BAYLIFF, W. H. 1950. The life history of the silverside *Menidia menidia* (Linnaeus). Chesapeake Biological Laboratory, Publication 90, Solomons, Maryland, USA.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. United States Fish and Wildlife Service Fishery Bulletin 53(74):302–304.

CLARK, F. N. 1925. The life history of *Leuresthes* *tenuis*, an atherine fish with tide controlled spawning habits. California Fish and Game Commission Bulletin 10:1–51.

CONOVER, D. O., AND B. E. KYNARD. In press. Experimental and field analysis of spawning periodicity and behavior of a northern population of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Environmental Biology of Fishes.

CONOVER, D. O., AND S. A. MURAWSKI. 1982. Offshore winter migration of the Atlantic silverside, *Menidia menidia*. United States National Marine Fisheries Service Fisheries Bulletin 80:145–150.

CONOVER, D. O., AND M. R. ROSS. 1982. Patterns in seasonal abundance, growth and biomass of the Atlantic silverside *Menidia menidia* in a New England estuary. Estuaries 5:275–286.

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

DAHLBERG, M. D. 1972. An ecological study of Georgia coastal fishes. United States National Marine Fisheries Service Fishery Bulletin 70:323–353.

DESYLVA, 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. University of Delaware Marine Laboratories Information Series, Publication 5.

GOODE, G. B. 1884. Natural history of useful aquatic animals. Part 3. The food fishes of the United States. Pages 448–467 *in* The fisheries and fishery industries of the United States, section 1. United States Commission of Fish and Fisheries, Washington, District of Columbia, USA.

HILDEBRAND, S. F. 1922. Notes on habits and development of eggs and larvae of the silversides *Menidia menidia* and *Menidia beryllina*. Bulletin of the United States Bureau of Fisheries 38:113–120.

HUBBS, C. 1976. The diel reproductive pattern and fecundity of *Menidia audens*. Copeia 1976:386–388.

LILEY, N. R. 1969. Hormones and reproductive behavior in fishes. Pages 73–110 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, reproduction and growth, bioluminescence, pigments, and poisons. Academic Press, New York, New York, USA.

MIDDAUGH, D. P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside *Menidia menidia* (Pisces: Atherinidae). Copeia 1981:766–776.

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

MIDDAUGH, D. P., G. I. SCOTT, AND J. M. DEAN. 1981. Reproductive behavior of the Atlantic silverside *Menidia menidia* (Pisces, Atherinidae). Environmental Biology of Fishes 6:269–276.

MIDDAUGH, D. P., AND T. TAKITA. 1983. Tidal and diurnal spawning cues in the Atlantic silverside *Menidia menidia*. Environmental Biology of Fishes 8:97–104.

ROBBINS, T. W. 1969. A systematic study of the silversides *Membras* Bonaparte and *Menidia* (Linnaeus) (Atherinidae, Teleostei). Doctoral dissertation. Cornell University, Ithaca, New York, USA.

SHAW, E. 1961. Minimal light intensity and the dispersal of schooling fish. Bulletin of de l'Institut Oceanographique (Monaco) 1213:1–8.

SHENKER, J., AND J. M. DEAN. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2:154–163.

TAYLOR, M. H., AND L. DIMICHELE. 1980. Ovarian changes during the lunar spawning cycle of *Fundulus heteroclitus*. Copeia 1980:118–125.