

SEMILUNAR REPRODUCTIVE CYCLES IN
FUNDULUS HETEROCLITUS (PISCES:
CYPRINODONTIDAE) IN AN AREA
WITHOUT LUNAR TIDAL CYCLES

Although lunar spawning rhythms are relatively common in species of shallow-water fish, semilunar reproductive cycles have been reported in a small but growing number of species (Korringa 1947; Johannes 1978). Species with the best documented semilunar gonad and spawning cycles include the California grunion, *Leuresthes tenuis*, (Clark 1925); Atlantic silversides, *Menidia menidia*, (Middaugh 1981); the tropical coral reef saddleback wrasse, *Thalassoma duperrey*, (Ross 1983); two tropical damselfishes, *Pomacentrus flavicauda* and *P. wardi*, (Doherty 1983), and gulf killifish, *Fundulus grandis*, (Greeley and MacGregor 1983); and the salt marsh mummichog, *Fundulus heteroclitus*, (Taylor et al. 1979; Taylor and DiMichele 1980). On the east coast of North America, *F. heteroclitus* move up onto marsh surfaces during high spring tides to spawn either in empty mussel (*Geukensia demissa*) shells or in the outer leaves of salt marsh plants (*Spartina alterniflora*) where oxygen levels are relatively high and sedimentation rates are relatively low (Able and Castagna 1975; Taylor et al. 1977; Kneib and Stiven 1978; Taylor and DiMichele 1983). Its eggs are extremely tolerant of desiccation and hatch on the next series of high spring tides. In addition, semilunar rhythms of larval hatching are well known for intertidal chironomid insects (Newmann 1978) and for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982).

In most cases, the proximal factors (sensu Giese and Pearse 1974) responsible for initiating and synchronizing these semilunar cycles are unknown. However, among the factors postulated as cues are tidal rhythms in water turbulence and hydrostatic pressures (Korringa 1947; Newmann 1978; Weld and Meier 1982; Ross 1983); tidal regimes in the habitat (Forward et al. 1982); photoperiod in combination with tidal fluctuations in water temperature (Miller et al. 1981), in combination with time of high tide (Middaugh 1981; Middaugh and Takita 1983), or in combination with interrupted current velocity (Middaugh and Hemmer 1984); and moonlight (Saigusa 1980). In addition to its wide distribution in coastal marshes with distinct lunar cycles of spring and neap tides, *F. heteroclitus* is abundant in extensive shoreline habitats and marshes of Chesapeake Bay, where tidal ranges are small and changes in water level caused by barometric pressure and wind frequently and unpredictably override lunar tidal

levels and obliterate semilunar tidal cycles. In the present study, we measured the reproductive activity of *F. heteroclitus* in an area without lunar tidal cycles in order to determine if semilunar reproductive rhythms occur. The occurrence of semilunar reproductive rhythms would suggest that the proximal cues regulating the reproductive cycles are not factors associated with changes in tidal levels, such as pressure, or turbulence of currents.

Methods

This study was conducted from May through August 1982 at a small tidal creek (Muddy Creek) which flows into the Rhode River (lat. 38°51'N, long. 76°32'W), a subestuary on the western shore of central Chesapeake Bay, located about 11.3 km south of Annapolis, MD. The creek bottom consists of fine clays and silts, and its banks are fringed by a cattail (*Typha angustifolia*) marsh. Water level was measured with a Honeywell¹ diffused silicon differential pressure transmitter (accurate to ± 1.238 cm) at a station operated by the U.S. Geological Survey on the Rhode River near the mouth of Muddy Creek about 1,000 m from the site where fish were sampled. Changes in water level at the monitoring station accurately reflect water levels at the sampling site (D. L. Correll² and R. L. Cory³). Measured daily high water levels were compared with predicted high tidal levels published for the Rhode River (National Oceanic and Atmospheric Administration 1981).

Fundulus heteroclitus is the most abundant fish in the creek (Hines unpubl. data). Fish were sampled every 2-3 d during the hours of 0730-1230, using unbaited minnow traps set just above low water level. Each sample consisted of 8-12 males and 8-12 females which were tested for readiness to spawn, and another 8-12 of each sex were taken to determine gonad indices. Readiness to spawn was determined in the field by applying gentle pressure from anterior to posterior along the ventral surface of the fish. Release of sperm or eggs was interpreted as the fish being ripe. The gonad index for each fish in the sample was determined by dissecting out the testes or ovaries and by drying the gonad and body to constant weight at 60°C and weighing them to the near-

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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est 1×10^{-5} g. The gonad index equals the (gonad weight/body weight) $\times 100$.

Results

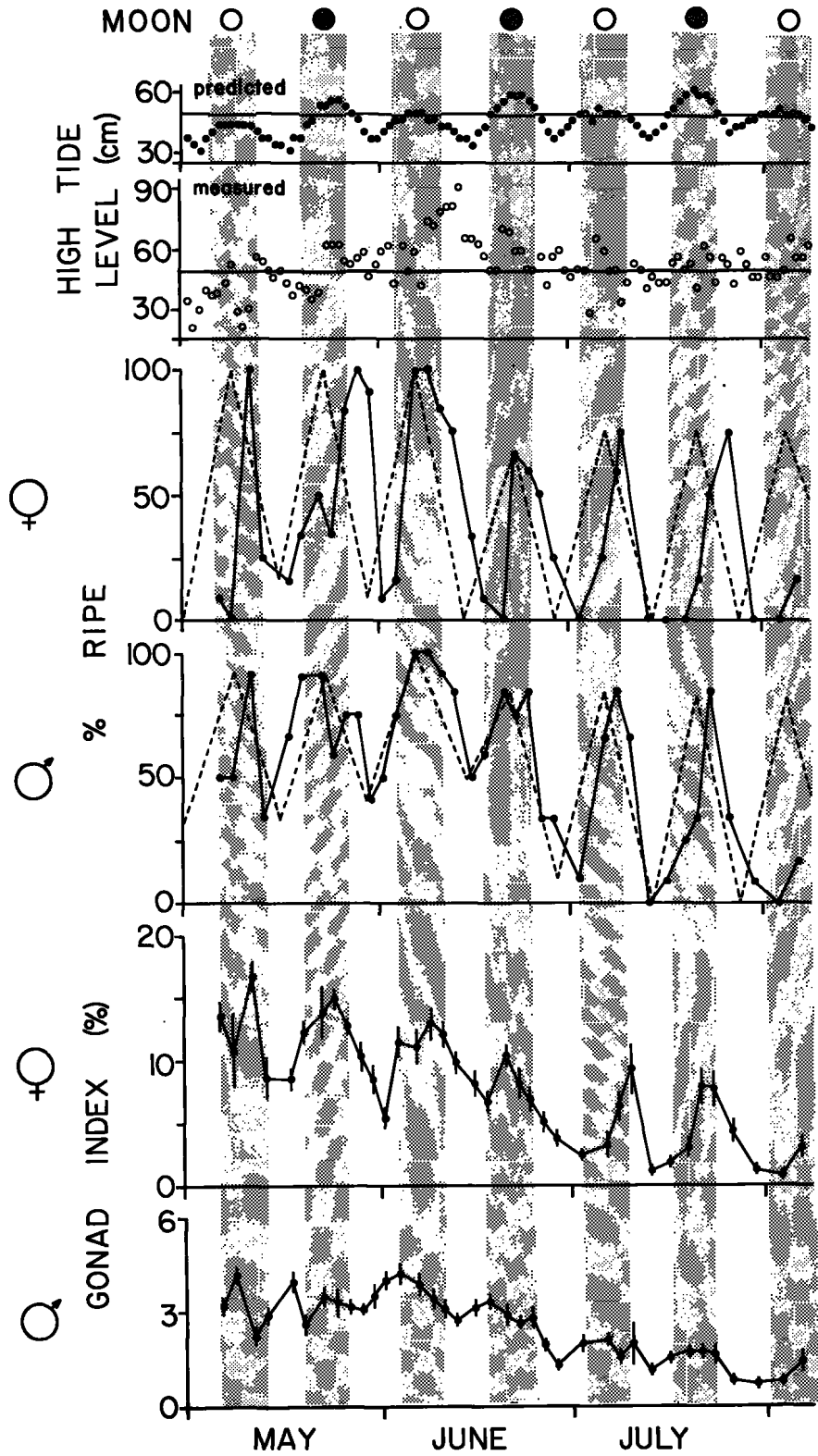
Although tides in the Rhode River subestuary exhibited an approximately semidiurnal rhythm, fluctuations in measured high tide level were not correlated with predicted high tide level (product moment correlation of log transformed data for daily predicted and measured high tide, $r = 0.111$; Student's t -test for $r \neq 0$, $P > 0.2$; Fig. 1). Moreover, time series spectral analysis (Thrall and Engelman 1981) showed that measured tides exhibited only a very weak peak in spectral density at a frequency of about 12.5 d rather than the strong peak of 7.5 d exhibited by predicted tidal cycles. Cross correlation between predicted and measured tides in bivariate spectral analysis showed low and variable coherence ($P > 0.05$). Similarly, linear association of the two variables was weak, with variable phase shifts and variable coefficients necessary to fit one variable to the other. In addition, the occurrence of tides sufficiently high to flood the marsh fringing the creek (i.e., tides > 46 cm) did not occur more frequently at night than during day (χ^2 test, $P > 0.2$), nor more frequently during any particular lunar phase (χ^2 test, $P > 0.4$). High tides did not occur consistently during any 2-h period of the 24-h day at the quarters of the new or full moons (χ^2 test, $P > 0.4$). Thus, water levels in the estuary were neither predictable in amplitude within the tidal range nor related in any obvious cyclical pattern to the lunar cycle.

However, both female and male *F. heteroclitus* showed distinct semimonthly cycles in readiness to spawn from May through August (Fig. 1). Females and males also exhibited a distinct semimonthly cycle of gonad size, although the cycle of male gonad index was not as pronounced as that of females, due to the small changes in size of the testes during spawning (Fig. 1). The cycles of spawning readiness in males and females were usually in phase with the lunar cycle. Comparisons of the observed frequencies of spawning readiness with frequencies predicted by cycles with perfect semilunar periods and the same amplitudes showed no significant differences in 27 of 37 d of observation for females and 33 of 37 d of observation for males (χ^2 test, $P < 0.05$). Observed frequencies of spawning readiness over the entire study period were not significantly different from frequencies predicted by the perfect semilunar cycles for either females or males (χ^2 test, $P > 0.2$). Although six out of six peaks of spawning readiness for males occurred during the 7 d surrounding new

or full moons, for females only four of the six peaks occurred during the first or last quarters of the moon, indicating that for the small numbers of peaks occurring during a reproductive season, readiness to spawn does not coincide with new and full moons (Fisher's Exact Test for number of spawning peaks occurring within the specified period, $P = 0.227$; Fig. 1). However, if the timing of the peaks in readiness to spawn is considered to lag 3.5 d after the new and full moons, then all peaks for males and females occurred within the 7 d surrounding the lagged period, indicating a significant synchronous semilunar cycle (Fisher's Exact Test on number of peaks occurring within the specified period, $P < 0.01$). Female spawning was correlated with male spawning (product moment correlation of arcsine transformed spawning frequencies, $r = 0.695$; Student's t -test for $r \neq 0$, $P < 0.001$). However, neither female nor male readiness to spawn was correlated with the measured tides (product moment correlation of arcsine transformed frequencies of spawning readiness with log transformed high tide measurements, $r = 0.184$ for females and $r = 0.272$ for males; Student's t -tests for $r \neq 0$, $P > 0.2$). Thus the semilunar cycles of spawning readiness of both sexes appeared to be synchronized, but not to be related to the tidal regime of the estuary.

The reproductive season of *F. heteroclitus* in the Rhode River-Muddy Creek estuarine system occurred from late April to September, when water temperatures were above 17°C (pers. obs.). Mean gonad indices of female and male samples declined during the season, both at the peak and at the spent phases of the semimonthly cycles (Female Gonad Index = $-0.124 \text{ Day} + 14.1$ and Male Gonad Index = $-0.035 \text{ Day} + 3.83$; Student's t -test for slopes $\neq 0$, $P \leq 0.05$; (Fig. 1)). The decline of mean gonad index during the season reflected two statistics. First, an increasing percentage of the population failed to initiate gonad recrudescence during successive cycles,

FIGURE 1.—Lunar phase, tidal levels, and reproductive cycles of *Fundulus heteroclitus* from May to August 1982 in a tidal creek on central Chesapeake Bay. Full moons (open circles) and new moons (solid circles) are indicated. Daily high water levels above mean low water are shown for measurements at the study site and for tidal levels predicted by National Oceanographic and Atmospheric Administration (1981). Horizontal lines indicate water level which floods the marsh adjacent to the Creek. The percentages of female and male fish which were ready to spawn are shown for each sample throughout the spawning season (solid lines), along with hypothetical spawning cycles with the same amplitudes and perfect semilunar periods in phase with the new and full moons (dashed lines). Gonad indices (mean \pm SE) for females and males are also plotted for each sample.



None of the female fish sampled on the May spawning peaks had undeveloped gonads (individual gonad indices were all > 10%), whereas many had undeveloped gonads on the July peaks (38% of the sample for gonad weights had individual indices < 5%, and 25% of the sample tested for spawning were not ripe). Second, gonad size of fish with developed gonads declined during the season. Mean gonad indices of females with developed ovaries of the May peaks were significantly greater than those of the July peaks (15% versus 9%, respectively) (Student-Newman-Keuls test of arcsine transformed data, $P < 0.05$).

Discussion

In *Fundulus heteroclitus* and *F. confluentus*, regulation of the annual reproductive cycle is apparently dependent on changing combinations of photoperiod and temperature (Harrington 1959; Day and Taylor 1982). The decline in gonad index during the season in the present study is consistent with a similar decline observed by Kneib and Stiven (1978) and Taylor et al. (1979) and suggests that, along with physical factors, energy availability may be limiting reproductive output late in the season. Weisberg (1981) found that supplemental food increased the gonad indices of *F. heteroclitus* in Delaware salt marshes. Histological evidence shows that primary oocytes in *F. heteroclitus* can undergo complete development in one biweekly spawning cycle (Taylor and DiMichele 1980), so lag time for recrudescence of spent gonads does not account for reduced reproductive activity late in the season. *Fundulus grandis* reproduces throughout the summer in some areas of the gulf coast (Greeley and MacGregor 1983), but shows bimodal reproductive activity in spring and fall with no reproduction in midsummer in shallow ponds (Waas and Strawn 1983).

In addition to *F. heteroclitus* (Taylor et al. 1979; Taylor and DiMichele 1980), semilunar spawning cycles occur in some populations of *F. grandis* (Greeley and MacGregor 1983), *F. similis* (Greeley 1982), *F. majalis* (Tedesco et al.⁴), and probably in *F. notatus* (inferred from observations of spawning behavior in Carranza and Winn 1954). Waas and Strawn (1983) measured a weak lunar, but not a semilunar cycle in populations of *F. grandis* in two nontidal ponds and a tidal creek with lunar tides frequently overridden by wind effects. The semilunar

spawning cycle in *F. grandis* has been induced in the laboratory during their reproductive season by interaction of photoperiod and tidal changes in water temperature shifting on a lunar cycle (Miller et al. 1981). Daily disturbances (netting) of *F. grandis* also apparently induces circadian gonadal responses (Weld and Meier 1982). Tidal rhythms in water turbulence and hydrostatic pressure have been postulated for lunar and semilunar reproductive rhythms in fish (Korringa 1947; Ross 1983) and for semilunar hatching in intertidal chironomid insects (Newmann 1978). Middaugh (1981) suggested that the biweekly coincidence of a high tide at the time of sunrise and/or a lunar cue may serve as a synchronizer for spawning of *Menidia menidia* in a South Carolina estuary. In contrast to *M. menidia*, which showed a precise reproductive response to diurnal tidal and lighting schedules (Middaugh and Takita 1983), *M. peninsulæ* exhibited a variable and labile response in which a combination of semidiurnal interruptions of current and diel light cues was optimal at inducing spawning synchrony (Middaugh and Hemmer 1984). However, this synchrony in *Menidia* spp. had a diel period, and the laboratory experiments were not run long enough to test for lunar rhythms. Semilunar rhythms of larval hatching are well documented for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982). Hatching in the mud crab, *Rhithropanopeus harrisi*, followed a semilunar and diurnal rhythm in populations from an estuary with semidiurnal and lunar tidal cycles, whereas hatching was not associated with lunar rhythms or tidal levels in an estuary with aperiodic tides (Forward et al. 1982). Moreover, Forward et al. (1982) induced circatidal rhythms in larval release in crabs from an estuary with irregular tides by transplanting them to an estuary with semidiurnal and lunar tides. However, Saigusa (1980) showed that the larval hatching cycle of a semiterrestrial crab *Sesarma haematocheir* is entrained directly by a moonlight cycle.

In the present study, in an area without a lunar periodicity in the tidal cycle, *F. heteroclitus* had a semilunar reproductive cycle which lagged the new and full moons by 3.5 d. Although the study area had tidal fluctuations with an approximately semidiurnal period, the diel timing of high tides with respect to photoperiod also did not appear to cue the semilunar reproductive cycle. Changes in currents associated with the diurnal tidal cycle may serve as a synchronizing cue for the time of spawning, as it does for *Menidia menidia* and *M. peninsulæ*. However, while identity of the cue remains unknown, the present study indicates that tidally mediated factors such

⁴Tedesco, M., A. H. Hines, and L. A. Wiechert. 1983. Semilunar gonadal cycles in *Fundulus majalis* (Pisces: Cyprinodontidae). Technical Report of Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037.

as turbulence, hydrostatic pressure, temperature, and salinity are not responsible for synchronizing the semilunar rhythm.

Hypotheses concerning the ecological consequences and adaptive significance of semilunar cycles of larval release in *Uca* spp. and other estuarine crabs have been discussed recently by Christy (1982). His analysis indicates that convergence among estuarine crab species in the semilunar timing of larval release results in rapid seaward transport of larvae, which minimizes the effects of lethal combinations of high temperature and low salinities or intense predation in the upper estuary. However, *Rhithropanopeus harrisi* completes its larval development within the upper reaches of estuaries and shows a variable cycle of hatching, depending on tidal predictability, which may be advantageous for retention of larvae within the estuary (Forward et al. 1982). Lunar spawning cycles of insular coral reef fish may have evolved to solve similar problems of larval dispersal away from predators while assuring return of the recruits to the adult habitat (Johannes 1978; Ross 1983). Semilunar spawning cycles of *Fundulus heteroclitus*, *Menidia menidia*, *Leuresthes tenuis*, and other fish which spawn in the upper intertidal zone (Taylor and DiMichele 1983; Middaugh 1981; Clark 1925) may have the adaptive advantage of removing spawning adults and eggs from subtidal predators. Although the eggs of *F. heteroclitus* are tolerant of desiccation (Able and Castagna 1975; Taylor et al. 1977), the major advantage of the spawning site appears to be higher oxygen levels and reduced sedimentation than in the creek (Taylor and DiMichele 1983). However, spawned eggs of *F. heteroclitus* and *M. menidia* are usually found in areas inundated daily by high tides (Middaugh 1981). In the present study, 62% of the days had tides which flooded the marsh (Fig. 1), where eggs are probably deposited in the bases of leaves of *Typha angustifolia* plants (see Taylor and DiMichele 1983). Although there may be additional advantages in areas with predictable tidal fluctuations with lunar periodicity, the major advantage of semilunar spawning rhythms in *F. heteroclitus* appears to be improved fertilization success afforded by synchronized spawning.

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Prey species are not uniformly distributed. Foraging efficiency, therefore, should be maximized when effort is concentrated in areas where prey are concentrated. Cetacean food is probably most concentrated in regions of high general productivity. Because the undersea topography may be a major influence on productivity, cetacean foraging patterns may be associated with the topographic patterns of the ocean floor (Hui 1979). I report here the occurrences of two species of pelagic odontocete cetaceans, the Pacific pilot whale, *Globicephala macrorhynchus*, and the common dolphin, *Delphinus delphis*, relative to seafloor topography and to diet. Although it is not clear if the genus *Delphinus* in this region is composed of two species or one species with two subspecies, the vast majority are *Delphinus delphis* (Banks and Brownell 1969; Evans 1975). If data from more than one species are included in this study, it is assumed that any interspecies difference in distribution relative to substrate was not significant to the analyses.

Methods and Results

This study was conducted in the Southern California Continental Borderland (Fig. 1) which consists of ridges, deep troughs, and basins (Chase 1968). There were 61 survey flights totaling 22,353 km. The flights were conducted at various times, all of them during midday (1000-1500) from 1968 through 1976. Totals of 1,057 pilot whales in 38 aggregations (in January, March, April, July, October, and December) and 47,105 common dolphins in 142 aggregations (in all months of the year) were observed. The survey methods have been previously described (Hui 1979).

The data for each species were not divided into temporal subsets as in Hui (1979), but were treated as whole sets. The distribution of each species was examined relative to depth and relative to change in depth. The method of analysis has been presented in detail elsewhere (Hui 1979).

Both pilot whales and common dolphins were distributed uniformly ($P > 0.10$) throughout the depth classes but not uniformly among the Contour Index (CI) classes ($P < 0.005$). For each species there were more observations than expected over the steepest bottom topography and fewer than expected over the flattest (Table 1).

I also compared the distribution of pilot whales