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Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators

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The ability of microscopic larvae to control their fate and replenish populations in dynamic marine environments has been a long-running topic of debate of central importance to understanding the ecology and evolution of life in the sea and managing resources in a changing global environment. After decades of research documenting behaviors that keep larvae close to natal populations, it is becoming apparent that larval behaviors in a broader spectrum of species promote long-distance migrations to offshore nursery grounds. Larvae must exert considerable control over their movements. We now show that larval emigration from estuaries is favored even over minimizing visibility to predators. An endogenous tidal vertical migration that would expedite seaward migration of Uca pugilator larvae was maintained experimentally across two tidal regimes. The periodicity of the rhythm doubled to match the local tidal regime, but larvae ascended to the surface during the daytime rather than at night. This process would conserve larval emigration but increase the visibility to predators across part of the species range. The periodicity of tidal vertical migration by Sesarma cinereum larvae failed to double and was inappropriately timed relative to both environmental cycles in the absence of a diel cycle. The timing system regulating tidally timed behaviors in these two species of crabs evidently differed. Phenotypic plasticity can conserve larval transport of both species when tidal and diel cycles are present. It may be widespread in the sea where diverse habitats are encountered across extensive species ranges.

Most marine animals spend weeks or months developing as larvae in the plankton, where large spatial and temporal variation in survival is a key determinant of the structure and dynamics of adult populations (1, 2). Large swings in larval recruitment have led to the prevailing belief that microscopic larvae are cast adrift in a vast, dynamic ocean with little behavioral control over their destinies. Larvae frequently are viewed as being overwhelmed by strong currents that carry them far from natal populations and a suitable habitat for completing the adult phase of the lifecycle (3–5). This view has remained entrenched, despite a long history of research demonstrating that larvae of some species develop within estuaries by overcoming net seaward flow, whereas others migrate far across the continental shelf and return to estuaries late in development (6, 7). These interspecific differences in larval transport are behaviorally mediated by the timing, duration, and amplitude of vertical migrations around the mean depth of larvae relative to seaward-flowing surface waters and landward-flowing bottom waters (8–10). Evidence for larval retention along open coasts and islands recently indicated that behavioral regulation of larval transport may be widespread (11). This finding has important implications for the dynamics and structure of populations and communities, as well as for fisheries management, design of marine reserve networks, spread of invasive species, and adaptation and extinction in the midst of global climate change (7).

Despite these advances, we lack a fundamental understanding of how complex suites of behaviors enable larvae to complete migrations between adult and larval habitats in diverse environments while minimizing losses from other sources of mortality across expansive species ranges. Here we describe a tradeoff that favors initial seaward migration over minimizing visibility to predators by contrasting larval behaviors of two estuarine species in different tidal regimes (Table 1).

The sun and tides provide reliable cues to time behaviors across species ranges. Changes in the periodicity of the tides and phasing with the diel (light–dark) cycle among the four tidal regimes of the world’s oceans necessitate changes in the timing of behaviors relative to these environmental cycles (12–15). In the most extreme case, the periodicity of tides doubles from 12.4 to 24.8 h between semidiurnal (two tides per day) and diurnal (one tide per day) regimes. The periodicity of behaviors must match the local tidal regime for tidally timed behaviors to be conserved across species ranges, but it would necessitate a change in the timing relative to the diel cycle (Table 1). Each phase of the two tides in the semidiurnal regime occurs during daylight and darkness every day. However, each phase of the one tide in the diurnal tidal environment can occur entirely in daylight or darkness depending on the time of year. The expression of one behavior or the other is precluded in this tidal regime. Behaviors regulating larval transport display a wide range of expression for species that span both tidal regimes because the periodicity of tidal vertical migrations must double from the semidiurnal to the diurnal tidal regime for larval transport patterns to be conserved (13, 15). The conservation of larval transport also would necessitate the suppression of diel vertical migrations in the diurnal tidal regime (13). Diel vertical migrations are widespread in aquatic systems and reduce visibility of larvae and other zooplankton to foraging fishes and exposure to UV-B radiation (UVBR) (16–18). The suppression of diel vertical migrations could reduce larval survival in the diurnal tidal regime (13).

Vertical migrations can be timed by directly responding to cues associated with diel and tidal cycles. However, larvae can possess internal clocks that enable them to anticipate and reliably time migrations in a noisy environment (8, 19, 20). These clocks are revealed by endogenous rhythms in behavior and physiology with free-running periods that approximate environmental cy-
In the semidiurnal tidal regime, larvae would undertake reverse tidal vertical migrations by rising twice per day during ebb tide (every 12.4 h) and diel vertical migrations by rising every 24 h at night. For larvae to undertake reverse tidal vertical migrations in the diurnal tidal regime, they would rise once per day (every 24.8 h) during the sole ebb tide, which primarily occurs in the daytime during the reproductive season (12, 13). In this tidal regime, the periodicity of vertical migration would double relative to the tidal cycle and the phasing would shift to the daytime. The timing of vertical migration across tidal regimes would be maintained relative to the periodicity and phase of the tidal cycle, rather than the diel cycle.

Endogenous and diel vertical migrations were observed in tall cylindrical columns in the absence of these environmental cycles every 2 h for 2 or 3 days. Trials were conducted early and late in the reproductive season in the diurnal tidal regime to detect differences in the timing of vertical migration relative to temporal shifts in the phase relationships of the two environmental cycles. Ebb tide occurred almost entirely in daylight during most of the reproductive season in the diurnal tidal regime. More of the ebb tide occurred in darkness early in the season. Larvae from two females were placed in separate columns for each trial, and the mean larval depth was calculated for each observation period. Tidal rhythms are difficult to detect, and several statistical techniques were used to ensure the accuracy of periodicity in the time series of larval vertical distributions (33, 34). Maximum entropy spectral analysis (MESA) generates an autoregressive model, and periodicities are determined by Fourier analysis (34). This method effectively identifies periodicity in tidal rhythms: The higher the amplitude of the peaks in the spectrum, the more likely their importance (33, 34). Autocorrelation was used in tandem with this test, although it can be less effective at identifying tidal rhythms. It has the advantage of providing 95% C.I. to indicate statistical significance (33–35). The periodicities found by using MESA and autocorrelation may result from tracking the diel cycle, tidal cycle, or both. Therefore, a repeated-measures ANOVA with tidal and diel cycles as factors were conducted to determine the environmental cycles tracked by larvae (Table 1).

Results

Endogenous diel vertical migrations were not expressed by larvae of either species (Figs. 2 and 3). The diel vertical migrations undertaken by both species in the plankton must be under exogenous control. Endogenous reverse tidal vertical migrations were expressed by larvae of both species from the semidiurnal tidal regime (Figs. 2a and 3a). Spectral analysis detected rhythms approximating the 12.4-h periodicity of the tidal cycle: 11.7 h for U. pugilator (Fig. 2b) and 11.4 h for S. cinereum (Fig. 3b). Autocorrelation determined that both rhythms were significant (Figs. 2c and 3c). ANOVA revealed that larvae occurred higher in the water column during the time of expected ebb than during the flood tide [supporting information (SI) Table 2]. Larval distributions were similar during the time of expected daylight and darkness.

In the diurnal tidal regime, the two species displayed different periodicities in response to the periodicity of the tidal cycle and the phasing of the diel cycle (Figs. 2a and 3a). The periodicity of vertical migration by U. pugilator larvae approximated that of the tidal (24.8-h) and diel (24-h) cycles throughout the reproductive season (23.9 h in August, 26.1 h in May) (Fig. 2b), and these
periodicities were significant (Fig. 2c). Larvae were highest in the water column during ebb tides in the daytime both early and late in the reproductive season (Fig. 2a and SI Table 2). Larval migrations were most closely associated with the diel cycle in August, when ebb tides occurred almost entirely during the daytime (Fig. 2a and SI Table 2). They were related to both cycles early in May, when ebb tides occurred in daylight and darkness. We cannot discern whether vertical migrations were associated with the tidal or diel cycle in this tidal regime because of the similar periodicities of the cycles and near synchrony of ebb tides and daylight. Larvae clearly rose during the same phase of the tidal cycle in both tidal regimes, but not the same phase of the diel cycle. Larval transport would be expedited on ebb tides at both locales, but avoidance of lighted surface waters would occur only in the semidiurnal tidal regime.

The periodicity of endogenous vertical migration by *S. cingulatum* larvae in the diurnal tidal regime matched a semidiurnal (12.4-h) tidal regime (12.1 h in August, 12.0 h in June, 12.4 h in May) (Fig. 3 a and b). Autocorrelation determined that these periodicities were significant only in May, when ebb tides partially occurred during darkness (Fig. 3c). Larvae were evenly distributed throughout the water column over diel and tidal cycles, except in August, when they were higher in the water column during the time of expected daylight than darkness (Fig. 3a and SI Table 2). Vertical migrations by larvae did not match the periodicity of the local tidal cycle, and they were weakly periodic and out of phase with the diel cycle.

**Discussion**

Endogenous timing of reverse tidal vertical migrations by newly hatched larval has been discovered for three species, including the European green crab (*Carcinus maenas*) (36). These migrations expedite larval transport by all three species from estuaries and bays to the continental shelf, where they develop (9, 10, 25–27). Investigators spent much of the last century debating how larval might replenish populations of estuarine species given that weakly swimming larval would be lost by net seaward flow (6). It was only later in the century that larval behaviors were found to facilitate offshore transport in some species (8–10, 26). It has become apparent that there is a behaviorally mediated continuum of larval migration between adult and larval habitats, ranging from retention in upper estuaries to migration to the edge of the continental shelf (9).

Reverse tidal vertical migrations expediting transport of *U. pugilator* from estuaries onto the continental shelf were conserved

![Figure 2](https://www.pnas.org/cgi/doi/10.1073/pnas.0704725105)
across tidal regimes by behavioral plasticity. Doubling of the tidal periodicity between the semidiurnal and diurnal regimes elicited a concomitant shift in the endogenous rhythms of larvae. Endogenous rhythms of reverse tidal vertical migration can be entrained by tides in embryos of subtidal species (36). These rhythms are initiated by females of semiterrestrial species, which must release their larvae in water (37). The timing matches the local tidal cycle immediately upon release in both cases. Reciprocal translocations of adults between tidal regimes in previous studies demonstrated unequivocally that changes in activity rhythms and the timing of larval release by *U. pugilator* and the congener *Uca thayeri* were plastic (21–23). Adults and larvae of *U. pugilator* most likely share the same timing system. This feature would enable them to track changes in the periodicity of tides across their geographic range and throughout the lifecycle. Although our study populations occurred in the same zoogeographic province (38), definitive evidence of plasticity in larvae awaits an experimental demonstration that they can entrain to a different tidal periodicity.

![Fig. 3. Endogenous rhythms, spectra, and correlograms of endogenous rhythms of vertical migration by *S. cinereum* larvae from semidiurnal and diurnal tidal regimes.](image-url)
The vertical migration rhythm of *S. cinereum* larvae was not plastic in constant conditions in the laboratory in contrast to *U. pugilator*. The periodicity of the rhythm in both tidal regimes matched that of tides from the semidiurnal tidal regime, rather than doubling in the diurnal tidal regime. The circatidal rhythm also does not appear to be adapted to local environments through genetic differentiation. This finding was evidenced by the mismatch between the periodicity of the rhythm and the tides in the diurnal tidal regime. The endogenous rhythms of larvae likely are plastic in the presence of a diel cycle as they are in adults. The presence of a diel cycle enabled egg-bearing females of both *S. cinereum* and *U. pugilator* held in the absence of a tidal signal to release larvae at the same appropriate times across their species ranges in previous studies (22, 39). Two approaches could reveal whether *S. cinereum* larvae from the diurnal tidal regime are capable of undertaking one long vertical migration per day in phase with ebb tide. Our study could be modified to include an ambient diel cycle, or the vertical distributions of larvae in the plankton could be profiled relative to diel and tidal cycles over consecutive days.

The results of the study species to constant conditions may reflect differences in the timing system. Two competing theories of the mechanism underlying tidally timed behaviors exist. First, tidal rhythms may be controlled by separate circatidal (~12.4-h) and circadian (~24-h) clocks (19). The circatidal oscillator would regulate activity rhythms in the semidiurnal tidal regime, resulting in two vertical migrations of equal amplitude each lunar day (~24.8 h). The circadian oscillator would regulate activity rhythms in the diurnal tidal regime, resulting in one vertical migration per lunar day. Rhythms also could be controlled by two lunar-day clocks that are coupled out of phase (20). In the semidiurnal tidal regime, each ~24.8-h oscillator would track one of the two tidal cycles per lunar day, resulting in two vertical migrations of equal amplitude. In the diurnal regime, only one of the lunar-day oscillators would regulate the rhythm of vertical migration. The other one would be suppressed, resulting in one vertical migration per lunar day. *U. pugilator* larvae evidently were able to track changes in the periodicity of tides in the two tidal regimes without an endogenous circadian oscillator. This finding is consistent with the single-clock (~24.8 h), rather than the dual-clock (~12.4 and 24 h), hypothesis. The dual-clock, rather than the one-clock, theory appears to be operating in the more terrestrial *S. cinereum*. Larvae were unable to track changes in the periodicity of the two tidal regimes in the absence of a diel cycle. There has been a long debate over whether circatidal rhythms are governed by one or two types of clocks. Our study suggests that both timing systems may exist even in these closely related families (40).

Expediting larval emigration from estuaries to the continental shelf by undertaking reverse tidal vertical migrations across tidal regimes is adaptive. It would minimize the physiological stress from large changes in temperature and salinity and encounters with planktivorous fishes throughout species ranges (27–30, 41, 42). Failure to do so by *S. cinereum* in the diurnal tidal regime would increase the risk of larval mortality (13). Even when larval transport is conserved across species ranges, the risk of larval mortality increases in the diurnal tidal regime. Larvae undertaking reverse tidal vertical migrations ascend into surface waters during the daytime, rather than at night, increasing their vulnerability to planktivorous fishes and UVBR (13).

Comparing responses of species to different tidal regimes is helping us understand the nature of timing systems regulating behavioral plasticity in the timing of larval release (14, 22, 23, 39) and larval vertical migrations. Behavioral plasticity in adults and larvae jointly conserve migration between adult and larval habitats while minimizing larval mortality. Phenotypic plasticity may be the most effective and common way for marine species with planktivorous larvae to adapt to environmental variation. That is, alterations in behavior, physiology, morphology, growth, and life history can be expressed by a single genotype when larvae recruit to a different habitat than did their parents and as environmental conditions change over time (12–14, 22, 43). Too rigid a system can restrict the species to one tidal regime because traits of adults and larvae would be well tuned in one tidal environment and poorly tuned in the others. Adaptation to local environments also may be less common in the sea because genetic differentiation often varies little across large spatial scales. It occurs only where gene flow is low or consistently strong selection overcomes high gene flow (44). Even if adaptation to local conditions were common, it is not clear that adult and larval crabs could time their activities any better than they already are. Environmental cycles that cue their behaviors and counter- vailing selective pressures enforcing them do not remain synchronized in time and space. The phasing of environmental cycles simply may be better tuned to the widespread semidiurnal tidal regime than less common ones. The lives of coastal organisms typically are timed by both tidal and diel cycles, and generalized phenotypic responses controlled by the two flexible timing systems described for crabs may be commonplace.

Determining how proximate and ultimate factors regulate the lives of animals across ecological landscapes is a powerful approach for revealing the costs and consequences of environmental change to survival and reproduction, the nature of timing systems, and how species adapt to predictable environmental change across geographic ranges of species. This approach has revealed the evolutionary importance of a behavioral tradeoff that conserves larval transport across species ranges.

**Methods**

Embryo-bearing females were collected in August 1998 in the semidiurnal tidal regime off the Atlantic Coast at an inlet of Indian River Lagoon in Fort Pierce, Florida. They also were collected between May and August from 1995 to 1998 in the diurnal tidal regime on the Gulf Coast at St. Joseph's Bay in Port St. Joe, Florida. Females were isolated in containers on seaward-facing sides under a natural photoperiod for ~48 h before they released larvae at night. Both adults and larvae were maintained at water temperatures and salinities that they experienced at collection sites. To reveal endogenous rhythms of vertical migration, 100 larvae from two females were transferred separately to transparent plastic columns (1.8 m × 10-cm diameter) before sunrise and were kept in darkness without food (45). A dim red light was used to count larvae, which are not sensitive to this portion of the spectrum. Larvae were counted in 1-cm vertical sections of the columns every 2 h for 2–4 days. Mean larval depth in the two replicate columns was calculated for each observation period. The center of larval distribution was determined by multiplying the number of larvae in each segment by the depth of the center of the segment and dividing by the total number of larvae counted (45).

Periodicity in the time series of larval vertical distributions was analyzed by using MESA and autocorrelation (33, 34). Trends and means were removed from data before analysis by performing a linear regression of mean depth over time and then subtracting the expected values from the observed values (35). Auto- correlation coefficients were calculated at 2-h (the sampling period) time-lag intervals. These coefficients were plotted as a function of time lag to generate correlograms. In random data, the mean of the correlogram is zero, and the standard deviation is 1/√n, where n is the sample size (35). Recurring peaks in correlograms that exceed 2√n/√T indicate significant periods at the 95% level, and these C.I. were displayed on correlograms (35). Repeated-measures ANOVAs with tidal and diel cycles as factors were conducted to determine the environmental cycles tracked by larvae (Table 1). Interaction terms were included in the model, except in trials conducted in the diurnal tidal regime in June and August, when ebb tides occurred almost entirely in daytime.

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