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Weakly synchronized larval release maintained in the presence of predatory fishes

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ABSTRACT

Many marine species minimize predation during hatching or spawning by releasing larvae or gametes synchronously during nocturnal spring ebb tides. Propagules are then rapidly transported away from high densities of predatory fishes into deeper waters under the cover of darkness. Females also suspend foraging in the presence of predators, but it is unknown whether they are able to delay releasing larvae. In a previous study, we found that larval release is only weakly synchronized to the safe period in a cold upwelling region, although the study was conducted on outdoor seawater tables in the absence of tides that reinforce endogenous rhythms. In this study, we experimentally determined whether larval release 1) is better synchronized in the field and 2) delayed in the presence of predatory fishes. Larval release was weakly synchronized to tidal amplitude, tidal and diel cycles, occurring from late flood to late ebb tide on both intermediate and spring tides during twilight as well as darkness. Weak synchrony likely arises because cold temperatures extend incubation of externally brooded embryos, increasing exposure to environmental variation. Larval release was not delayed in the presence of predatory fishes; nor was refuge use or other behaviors of females altered by fishes. Behaviors were not affected by predators presumably because larvae are already being released near the safe period from refuges. Our results likely apply to other cold regions of the world, but it remains to be determined whether predators alter the activities of nonovigerous female and male shore crabs, which may not spend as much time in refuges as ovigerous females, potentially resulting in cascading effects on communities.

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1. Introduction

Reproduction by many species of coastal marine animals occurs when predation on adults or offspring is minimized relative to diel, tidal and tidal amplitude cycles (Morgan, 1995; Morgan and Christy, 1995; Thurman, 2004). Reproduction occurs at night when parents and offspring are least visible to predators (Hovel and Morgan, 1997; Morgan, 1990). It also occurs near high tides and especially spring high tides, when intertidal species can release larvae or gametes from the safety of refuges (Christy, 1986; Morgan, 1996a; Morgan and Christy, 1995) and larvae or gametes are transported by ensuing ebb tides to deeper waters where fewer predators occur (Hovel and Morgan, 1997; Johannes, 1978; Morgan, 1995). Thus, reproduction by many crabs and fishes is synchronized to coincide during the safest phases of all three environmental cycles: nocturnal, spring, and high tides (Morgan, 1995; Thurman, 2004).

In upwelling regimes, larval release by crabs appears to be only weakly synchronized (high variance around the mean) to the safe period (Christy, 2003, 2011; Kerr et al., 2012; Morgan et al., 2011).

Cold upwelled water and exposure to variable temperatures during low tide increase the incubation time of embryos, which in turn, likely increases variation in the timing of hatching. In warmer upwelling regions, female crabs may adjust the timing of mating, regulate their depth in burrows or choose the width of burrows during courtship to compensate for variation in development rates of embryos arising from small changes in temperature (Christy, 2011; Christy et al., 2001; Kerr et al., 2012; Reaney and Backwell, 2007). However, these compensatory behaviors may be less effective when cold temperatures lengthen incubation periods, especially for species that live in depressions under rocks rather than in burrows (Christy, 2003; Morgan et al., 2011).

Although the proximal and ultimate factors regulating reproductive synchrony have been well studied in crabs, it remains unknown whether females can delay releasing larvae in the presence of predators (Morgan, 1995). Predators are well known to affect foraging by many animals with cascading nonconsumptive indirect effects on communities (Schmitz et al., 2004; Trussell et al., 2006; Werner and Peacor, 2003). Further, in some species, such as snails and amphibians, the presence of predators induces embryos to hatch raising the possibility that crustacean embryos may potentially be able to chemically detect predators (Blaustein, 1997; Miner et al., 2010; Warkentin, 2011a, 2011b). Females even may delay releasing larvae in the presence of predators if embryos that are ready

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to hatch can be postponed. Predatory fishes abound along shorelines, and females, embryos and larvae all may be vulnerable during larval release (Hovel and Morgan, 1997; Morgan, 1990; Yoklavich et al., 1991).

We determined the effectiveness of intertidal crabs to regulate the timing of larval release in cold upwelling regimes in the presence of predators. Our previous study showing that larval release by several species of crabs was weakly synchronized to the safe period in a cold upwelling regime was conducted on outdoor seawater tables in the absence of tides, and it is possible that larval release could be more synchronous in natural populations where tides reinforce endogenous rhythms (Morgan et al., 2011). To test this hypothesis, we determined the timing of larval release relative to the safe period in the field. We then experimentally determined whether the presence of predatory fishes substantially delays larval release in the laboratory. We tested two species of fishes, one that preys on adult crabs and a second species that feeds on larvae, to determine whether predation on adults or larvae cause females to delay the release of larvae. We concurrently observed whether fishes altered foraging and other behaviors of females to determine whether ovigerous females were generally threatened by these fishes.

We chose the lined shore crab, *Pachygrapsus crassipes* (Randall 1839), because this high intertidal species should release larvae more synchronously relative to the safe period than species that live lower on the shore (Morgan, 1995; Morgan and Christy, 1995; Thurman, 2004). *P. crassipes* inhabits exposed rocky shores and estuaries where it primarily feeds on algal films and spawns from April through September brooding embryos for 16–29 d (Hiatt, 1948). Average carapace width of female and male *P. crassipes* is 40 and 47 mm, respectively, and adult density varies among estuaries (Morgan et al., 2006). The predator on adults was the cabezon, *Scorpaenichthys marmoratus* (Ayers 1854), which feeds on *P. crassipes* and other benthic invertebrates and fishes (O'Connell, 1953). The planktivore was the three-spined stickleback, *Gasterosteus aculeatus* (Linnaeus 1758), which preys on *P. crassipes* larvae and other zooplankton (Rasmuson and Morgan, 2013).

2. Materials and methods

2.1. Timing of larval release

We determined the timing of larval release by *P. crassipes* relative to the lunar, tidal amplitude, tidal and diel cycles for 30 d (June 14–July 13, 2006) in the field. Ovigerous *P. crassipes* ($n = 60$) were captured by hand and placed in a mesocosm that was secured to the substrate near a large population of *P. crassipes* in Bodega Harbor, California. Crabs that released larvae during the first 15 d of the study were replaced with 30 ovigerous females to ensure that sufficient numbers of ovigers were present to release larvae during the second half of the study. Seawater temperature ranged from 9.4 to 15.8 °C with a mean temperature of 11.8 °C during the study.

The mesocosm ($1 \times 0.5 \times 0.5$ m) was constructed of plastic. A lid was constructed of clear Plexiglass covered with Vexar mesh (0.5 cm) to allow sunlight to enter and heat to escape the mesocosm. Ninety two holes were drilled in the walls of the mesocosm (5-cm diameter) and were covered with Nitex mesh (135 μ m) to permit water exchange while excluding most zooplankters and all predators and containing newly released larvae. Rocks amid the adjacent natural population of crabs were collected and placed inside the mesocosm to provide cover and food for these herbivorous crabs. Temperature loggers (Tidbit, Onset Inc.) were secured inside and outside of the mesocosm to ensure that temperatures inside the mesocosm were similar to ambient temperatures. A manual submersible pump was attached to the mesocosm, and seawater (240 l) was pumped every 30 min during high tides following inundation (tidal height = 1.25 m). Pumped seawater was discharged through a plankton net (333 μ m) that was suspended in a bucket. Before the start of each daily sampling period, the mesocosm was pumped to clear any larvae that might have been released between observation times. Mechanical difficulties precluded sampling for one

day (June 25). Larvae from each 30 min sample period were preserved separately in 95% ethanol, and the amount of larvae released was quantified volumetrically (ml). An average of seven (range 2–11) samples were collected during each sampling period.

Whether larval release occurred relative to the diel (24 h) cycle was determined using a G-test after categorizing data as daylight, nighttime and twilight (sunset and sunrise ± 90 min). Larval release relative to semilunar (15 d), tidal amplitude (12–17 d) and tidal (12 h) cycles in the mixed-semidiurnal tidal regime was analyzed using circular statistics, Rayleigh test. For significant peaks of larval release, we related means and standard deviations to the phasing of environmental cycles to determine the timing and degree of synchrony. During our one-month study, larval release was determined relative to two semilunar cycles, two tidal amplitude cycles, 30 diel cycles and 60 tidal cycles.

2.2. Affect of predators on the timing of larval release

We conducted a laboratory experiment to determine whether 1) the presence of predators reduces the number of female crabs that release larvae, 2) females delay larval release until after predators leave and 3) predators of females or their larvae are more likely to affect the timing of larval release. The timing of larval release was expected to occur near high tide, when all intertidal species of crabs worldwide release larvae (Morgan, 1995; Thurman, 2004). However, the precise timing of larval release varies among individuals, especially in this cold upwelling regime where larval release by *P. crassipes* is weakly synchronized to the tidal cycle (Morgan et al., 2011). The present study confirmed that peak larval release occurred within the first 3 h following high slack tides. Therefore, we expected to be able to detect a delay in the timing of larval release from the first 3 h to the last 3 h of ebb tide in the presence of predators.

The experiment was conducted during July and August 2006. Ovigerous *P. crassipes* were collected by hand during low tide from the population in Bodega Harbor, and fishes were seined from an adjacent eelgrass bed. The crabs and both species of fishes (*S. marmoratus* and *G. aculeatus*) were held separately in flow-through outdoor tanks under ambient light conditions. A simulated tidal cycle coincided with local tides to reinforce endogenous tidal rhythms and water level oscillated (± 18 cm). Continuous water flow maintained ambient water temperature and oxygen levels. Tanks were filled with rocks and gravel that were collected together with female crabs to provide a familiar refuge.

Embryos of all crabs were inspected before each trial to ensure that they were fully developed and ready to be released. These females were placed into experimental tanks for observation during the morning of each trial. Because larval release by *P. crassipes* was not highly synchronous, the number of ovigerous crabs that were ready to release larvae varied from day to day ranging from three to eight crabs per tank. The number of fishes in each of three predator treatments remained constant throughout the experiment: two juvenile *S. marmoratus*, five adult *G. aculeatus* and no predators. More *G. aculeatus* than *S. marmoratus* were placed in each tank, because the latter species is smaller and more prevalent (Rasmuson and Morgan, 2013). Three replicate aquaria (110 l) were used for each of the three treatments resulting in a total of nine tanks per trial. The small tanks created a high-density environment to ensure encounters between predators and prey. Ten trials were conducted on different nights resulting in 30 replicates per treatment.

Table 1

Timing of observations and the introduction and removal of fishes to determine whether *P. crassipes* delayed releasing larvae relative to high tide or altered other behaviors in the presence of predators.

Time relative to high tide	1 h before	High tide	3 h after	6 h after
Observation period	X		X	X
Predator		Introduced	Removed

Fig. 1. Timing of larval release (bars) by *P. crassipes* relative to diel, tidal amplitude and lunar cycles from June 13 to July 13, 2006. Each bar represents the volume (ml) of larvae released during each 30-min period, and the absence of bars (when the mesocosm was submerged) indicates no larval release. Solid lines represent nocturnal tidal height and dashed lines represent daytime high tide. The horizontal dashed line is the tidal height when the mesocosm was inundated (1.25 m). Full, new and quarter moons are represented by filled, open and half-filled circles. ND indicates that data were not collected. Sixty ovigerous females were placed in the mesocosm at the beginning of the study and 30 additional ovigerous females were added to the mesocosm 15 d later.

Trials were conducted at night during the time of local high tides when *P. crassipes* releases larvae (Morgan et al., 2011). We recorded the number of ovigerous crabs remaining and releasing larvae 1 h before

high tide, 3 h after high tide and 6 h after high tide (Table 1). To determine whether ovigerous crabs spent more time in refuges in the presence of predators, we recorded whether they occurred 1) in the

Fig. 2. Total larval release (ml) by *P. crassipes* every 30 min relative to the timing of predicted high tide over 29 d. No larval release occurred from 180 to 90 min before high tide. Sixty ovigerous females were placed in the mesocosm at the beginning of the study and 30 additional ovigerous females were added to the mesocosm 15 d later.

open on gravel fully visible to fishes, 2) in crevices of rocks partially visible, and 3) hiding under rocks hidden from view. *P. crassipes* displayed four behaviors during the course of our study 1) stationary filter feeding, 2) picking food from the substrate, 3) fighting or 4) walking. The number of individuals in each habitat displaying each behavior was recorded during each of three observation periods. Observations were conducted in darkness with a red light to minimize disturbing crabs, which do not see well at this wavelength (Cronin and Forward, 1998). Indeed, briefly shining a red light on crabs did not alter their behavior during our experiments. Predators were introduced at high slack tide (1 h after the first observation) and removed 3 h later just after the second set of observations was recorded (Table 1). Predators appeared to be foraging and behaving normally after being introduced to the experimental tanks. All fishes survived the experiments. Thus, during each observation period, the number of females that released larvae was recorded along with habitat use and other behaviors of each individual to determine the effect of predators on females that were ready to release larvae.

Our study was designed to determine whether the presence of predators may suppress and delay larval release in natural populations rather than to adhere to strict experimental design protocol for its own sake. Including multiple predatory fishes and crabs in arenas can be viewed as violating the assumption of independence (Petersen and Renaud, 1989). However, crabs live in dense aggregations and planktivorous fishes forage in schools. Ovigerous crabs may not perceive a single small planktivorous fish as a sufficient threat to delay releasing thousands of larvae into the water column, but a school of fishes may be perceived as a threat. Furthermore, the release of hatching pheromones stimulates vigorous release of larvae (Forward et al., 1987) and may synchronize larval release among neighbors.

The number of ovigerous crabs releasing larvae in each predator treatment during each observation period was analyzed using generalized linear models with a binomial distribution and a logit link function (Crawley, 2012). The model included each of the three predator

Table 2

Rayleigh statistic for the timing of larval release ($\pm$ SD) by *P. crassipes* relative to tidal, tidal amplitude, and lunar cycles. We reported the mean and standard deviation for significant peaks of larval release.

Factor	Mean $\pm$ SD	Z	N
Tidal cycle	High tide $\pm$ 60 min	0.6523***	48.5
Tidal amplitude cycle	Spring high tides $\pm$ 3.25 d	0.2767*	48.5
Lunar cycle	Asynchronous	0.1667	48.5

N = total volume (ml) of larvae released during the course of the study.

* $P < 0.05$.

*** $P < 0.001$.

Fig. 3. Total volume (ml) of larvae released by *P. crassipes* each day (bars) relative to lunar cycle and daily and nightly maximum amplitude tides over 29 d. Dashed lines denote maximum amplitude tides that occurred during daylight and solid lines represent maximum amplitude tides that occurred at night. Rapid changes in tidal amplitude occurred when daytime high tides switched to night and vice versa. Full, new and quarter moons are denoted by filled, open and half-filled circles. ND indicates that data were not recorded. Sixty ovigerous females were placed in the mesocosm at the beginning of the study and 30 additional ovigerous females were added to the mesocosm 15 d later.

experiments (adult predator, larval predator and control) as well as the three different time periods. Habitat use and behavior were analyzed as percentages, because the number of crabs was not consistent among trials. The percentage of crabs in each habitat and displaying each behavior based on predator treatment was analyzed using the nonparametric Scheirer–Ray–Hare extension of the Kruskal–Wallis test (Sokal and Rohlf, 2012). Time period was not included in the analyses of habitat and behavior because the Scheirer–Ray–Hare extension is limited to two factors.

3. Results

Most (96%) crabs released larvae at twilight or night (Fig. 1, G-test, $P < 0.001$). Larval release occurred near high slack tide and spring tides (Figs. 1 & 2, Table 2). Larval release was weakly synchronous relative to the tidal amplitude cycle (± 3.25 d), peaking twice during spring tides at night and three times during intermediate amplitude tides of similar tidal height during the daytime and nighttime (Figs. 1 & 3, Table 2). Larval release was not synchronized to the semilunar cycle (Figs. 1 & 3, Table 2).

Fig. 4. Percentage of the total number of *P. crassipes* releasing larvae 1 h before high slack tide (just before the introduction of the predator, bottom black bar), 3 h after simulated high slack tide (just prior to the removal of the predator, middle dark gray bar) and 6 h after the simulated high slack tide (3 h after the predator was removed, top light gray bar) in the presence and absence of fishes that consume adult crabs (*S. marmoratus*) or their larvae (*G. aculeatus*). Thirty trials were conducted for each predator factor over 10 d. A total of 493 crabs were observed.

Table 3
Generalized linear model structure of the interaction of observation period and predator modeled as categorical factors using a binomial distribution with logit link.

Coefficients	Estimate	SE	Z	P
1 h before high tide	−1.829	0.229	−7.963	<0.001
3 h after high tide	−3.657	0.506	−7.222	<0.001
6 h after high tide	−5.063	1.003	−5.048	<0.001
Larval predator	−0.012	0.321	−0.038	0.969
Adult predator	−0.159	0.331	−0.480	0.631
3 h after high tide × larval predator	0.534	0.713	0.749	0.454
3 h after high tide × larval predator	0.656	1.271	0.516	0.606
6 h after high tide × adult predator	−0.179	0.840	−0.213	0.831
6 h after high tide × adult predator	1.750	1.150	1.522	0.128
Null deviance: 1702.2 for 270 degrees of freedom				
Residual deviance: 258.3 for 261 degrees of freedom. AIC: 378.23				

The presence of predatory fishes did not alter the timing of larval release. More larvae were released soon after high slack tide in both the absence and presence of predatory *S. marmoratus* and planktivorous *G. aculeatus* (Fig. 4, Table 3). Crabs did not delay releasing larvae as fishes swam by nor did fishes linger near crabs releasing larvae.

Predatory fishes also did not alter habitat use or other behaviors of ovigerous females. Ovigerous females spent about 78% of their time hiding underneath and in crevices of rocks in the presence and absence of *S. marmoratus* and *G. aculeatus* (Fig. 5, Table 4). They spent about 88% of their time filter feeding, and far less time was spent benthic feeding, walking and fighting in both the presence and absence of predatory fishes (Fig. 6, Table 4). Nevertheless, *S. marmoratus* was a threat because they ate two crabs during predation trials.

4. Discussion

Larval release by *P. crassipes* was weakly synchronized to tidal amplitude, tidal and diel cycles in the field where entraining cues reinforced endogenous rhythms as we found during our previous laboratory study conducted in the absence of tides (Morgan et al., 2011). In both studies, most *P. crassipes* not only released larvae near spring high tides in twilight and darkness, but they also released larvae near intermediate amplitude high tides during the day and night when the height of daytime and nighttime tides was similar. The timing of larval release by a congener (*Pachygrapsus transversus*) in both a warm upwelling, semidiurnal tidal regime and a warm nonupwelling, mixed semidiurnal tidal regime was similar (maximum and intermediate amplitude tides, before and after high slack tides, twilight and darkness; Morgan and Christy, 1994), suggesting that larval release may not have been mistimed by *P. crassipes*. Releasing larvae during maximum and intermediate amplitude high tides enables females to release larvae from

Fig. 5. Percent time spent by ovigerous *P. crassipes* filter-feeding (bottom black bar), picking food from the substrate (top dark gray bar), walking (middle upper light gray bar) and fighting (middle lower white bar) in the presence and absence of fishes that consume adult crabs (*S. marmoratus*) or their larvae (*G. aculeatus*). Thirty trials were conducted for each predator factor over 10 d. A total of 493 crabs were observed.

Table 4
Scheirer–Ray–Hare extension of the Kruskal–Wallis test determining the effect of a predatory fish (*S. marmoratus*) and planktivorous fish (*G. aculeatus*) on habitat use and four other behaviors (filter feeding, substrate feeding, walking and fighting) of ovigerous crabs. Larval release was not included in the analysis because it occurs too briefly to be frequently observed. Analyses were conducted on ranked percentages, because the number of ovigerous females varied over time. Ninety trials were conducted (30 for each factor) using a total of 493 crabs.

Response variable	df	SS	H	P
Habitat use				
Predator	2	4234.0	0.223	NS
Habitat	2	1,743,818.1	91.775	<0.001
Predator × habitat	4	18,344.9	0.965	NS
Other behaviors				
Predator	2	233.0	0.0072	NS
Behavior	4	11,043,583.0	339.803	<0.001
Predator × behavior	8	25,622.0	0.784	NS

NS = P > 0.05.

their refuges in the upper intertidal zone while larvae are rapidly transported from high densities of predatory fishes into deeper waters (Hovel and Morgan, 1997; Morgan and Christy, 1995; Morgan et al., 2011). However, larval release by *P. crassipes* was less synchronous relative to the tidal amplitude and tidal cycles than for the congener, suggesting that the cold temperatures in the upwelling regime increased variation relative to target windows for releasing larvae. Cold upwelled water increases the incubation time of embryos and exposure to variable temperatures during low tide, which in turn, increases variation in the timing of hatching (Christy, 2011; Morgan et al., 2011).

Releasing larvae away from the safe period should increase fish predation in cold upwelling regimes (Morgan et al., 2011). In a companion study, predation was indeed highest on newly released larvae of *P. crassipes* and other shore crabs when larval release peaked away from the safe period (intermediate amplitude ebb tides in twilight; Rasmuson and Morgan, 2013). However, predation was not as high as expected, because planktivorous fishes were not always present while females were releasing larvae. Unlike amphibians and marine snails (Miner et al., 2010; Warkentin, 2011a, 2011b), the presence of predators did not induce large variation in the timing of hatching by *P. crassipes*. A key difference between these taxa and crabs is that the crab embryos are attached to the female so that the timing of hatching is at least partially under her control. Hatching of crab embryos releases a pheromone into the water that initiates vigorous pumping of the abdomen by the female to expedite the release of the brood within minutes (De Vries and Forward, 1991). Females will release larvae into the water upon being transferred to a container or even cupped in the palm of your hand (S. G. Morgan, personal observation). Once

Fig. 6. Percentage of crabs occupying rocks (bottom black bar), crevices (middle dark gray bar), and gravel (top light gray bar) in the presence and absence of fishes that consume adult crabs (*S. marmoratus*) or their larvae (*G. aculeatus*). Thirty trials were conducted for each predator factor over 10 d. A total of 493 crabs were observed.

one or more of the thousands of embryos in the brood hatches, the pheromone cueing stereotypical pumping of the abdomen apparently overrides defensive behaviors in response to disturbance or the presence of predators. Hence, predatory fishes may not cause large disruptions in the timing of larval release in natural populations, because releasing larvae during the safe period already minimizes predation.

Ovigerous *P. crassipes* also did not alter other behaviors in the presence of predators, including filter-feeding, benthic foraging, walking and fighting, even though *S. marmoratus* ate females twice during the study. This finding was somewhat unexpected, because predators are well known to suppress foraging by a wide variety of taxa often resulting in cascading effects on communities (Schmitz et al., 2004; Trussell et al., 2006; Werner and Peacor, 2003). However, ovigerous crabs spent most their time in refuges regardless of whether predators were present or absent (~78%), even though this species is most active at night when our study was conducted (Hiatt, 1948; Michaels, 1988). Activities of ovigerous crabs were not affected by predators, because they spent so much time in the safety of refuges anyway.

The absence of a predator effect on the timing of larval release and other behaviors of ovigerous females was not due to limitations of our experimental design. The timing of larval release and other behaviors were quite similar in the presence and absence of predators so that increasing replication is unlikely to alter results. Potential lingering scent after the removal of predators in our flow-through tanks was not an issue because results were similar in predator and control treatments. Further, larval release during late ebb tide was also common during our field experiment as well as a companion study in natural populations (Rasmuson and Morgan, 2013). Finally, a previous study also concluded that behaviors of *P. crassipes* are not altered simply by holding them in the laboratory (Bovbjerg, 1960).

In conclusion, larval release by crabs in cold upwelling regions is weakly synchronized to the safe period, likely due to increased exposure to temperature variation during long embryonic development (Kerr et al., 2012; Morgan et al., 2011). The timing of larval release by shore crabs in cold nonupwelling regions of the world should be examined to determine whether weak synchrony also occurs there, especially in mixed tidal regimes that are more challenging to track than the regular phasing of environmental cycles in semidiurnal tidal regimes (Morgan, 1996a, 1996b; Morgan and Anastasia, 2008; Morgan and Christy, 1994). We also provided the first evidence that predatory fishes do not alter the timing of larval release or other activities of ovigerous females, which spend much of their time in the safety of refuges, despite recent work demonstrating that planktivorous fishes do consume *P. crassipes* larvae (Rasmuson and Morgan, 2013). Because peak release during the safe period already minimizes predation on larvae, females apparently cannot further increase survival of either adults or larvae by delaying release in response to passing predators. Repeating the study in a warm climate, where larval release by many species is highly synchronized, would make it easier to detect delayed larval release in the presence of predators, thereby providing an even stronger test of the hypothesis. Finally, it remains to be determined whether predators alter the activities of nonovigerous female and male shore crabs, which may not spend as much time in refuges as do ovigerous females, potentially resulting in cascading effects on communities.

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