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DECREASED TEMPERATURE RESULTS IN DAYTIME LARVAL RELEASE BY THE FIDDLER CRAB *UCA DEICHMANNI* RATHBUN, 1935

Kecia A. Kerr [1,2,3,*]

[1] Department of Biology, McGill University, 1205 Docteur Penfield, Montréal, Québec, Canada H3A 1B1
[2] Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá
[3] McGill-STRI Neotropical Environment Option (NEO), Faculty of Science, McGill University, Montréal, Québec, Canada H3A 2T6

ABSTRACT

Many crabs release their larvae during large amplitude high tides at night to reduce predation by fishes. These "safe" tides often occur within a few hours of dawn, therefore crabs targeting these tides are vulnerable to releasing larvae during daylight if a decrease in temperature extends incubation by a few days. *Uca deichmanni* Rathbun, 1935 release larvae during the large amplitude tides, but the timing of larval release with respect to the tidal and diel cycle was previously unknown. This species released larvae exclusively during the high tide, approximately two hours before sunrise, in warm conditions in the laboratory. In cold water, females released larvae primarily during the high tide, but many released during daylight (55%). During cold conditions in the field, 35% of females released larvae on days when the morning high tide occurred during daylight. These females or their larvae may therefore have been exposed to higher risk of predation by diurnally feeding predators.

KEY WORDS: larvae, predation risk, reproductive cycles, temperature, timing of reproduction, upwelling

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INTRODUCTION

Many species of brachyuran crabs demonstrate strong cycles of larval release with an impressive ability to target larval release with particular moments in tidal and diel cycles. The most prevalent timing of larval release, especially for intertidal crabs (83% of species surveyed), is during large or maximum amplitude (spring) high tides at night (Christy, 2011). Predation by fishes on newly released larvae is higher during the day in many habitats (Hovel and Morgan, 1997; Morgan and Christy, 1997; Kerr et al., 2014a). This timing of larval release therefore likely reduces the risk of predation on females and larvae by diurnally feeding fishes that are abundant nearshore (Morgan, 1990, 1995; Morgan and Christy, 1995, 1997; Hovel and Morgan, 1997; Kerr et al., 2014a). A few crab species nevertheless release larvae during both day and night, or release during the day, if the largest amplitude tides do not occur at night (Morgan and Christy, 1995; Kellmeyer and Salmon, 2001; Yamaguchi, 2001; Christy, 2011; Rasmuson et al., 2014). In addition, there are conditions under which females may be unable to match the timing of larval release with the best tides, the nocturnal high tides with large amplitude, and must release during suboptimal tides. For example, as temperature changes, crabs may not be able to compensate for the effects of temperature on incubation period and the timing of hatching may shift by several days (Kerr et al., 2012).

The safest tides for larval release, the maximum or large amplitude nocturnal high tides (Christy, 2011), occur for a few days approximately biweekly in areas with semidiurnal or mixed semidiurnal tides, such as along much of the coasts of the Americas. Maximum amplitude high tides, the targeted period for larval release, tend to occur just before dawn and dusk in Panama. Since the high tide occurs approx. 40 min to 1 hour later each day, high tide releases that occur several days after the maximum amplitude tides will occur after sunrise or sunset. Embryos that develop at relatively low temperatures have longer incubation periods and may not be ready to hatch until several days after the maximum amplitude tide. Once the morning high tides occur after sunrise, crabs could potentially avoid releasing larvae during the day by switching to the early evening high tide, thus maintaining release during the cover of darkness.

The ecology and behavior of *Uca deichmanni* Rathbun, 1935 is relatively unknown. This species exhibits cycles of courtship and larval release that is synchronized with the largest amplitude tides, but the timing of release of larvae relative to tidal and diel cycles has not been reported (Zucker, 1983; Kerr et al., 2012, 2014b). If *U. deichmanni* release their larvae at the time of the high tide as expected, they might avoid hatching during daylight when conditions cool by switching from the morning high tide to the evening high tide. I examined the timing of the release of larvae by females kept in the laboratory relative to tidal and diel cycles. Females were held in: 1) ambient, warm conditions

* Current address: Australian National University, Research School of Biology, Division of Evolution, Ecology and Genetics, Canberra, ACT 2601, Australia. Mailing address: 9807 78 Avenue NW, Edmonton, AB, Canada T6E 1N4. E-mail: kecia.kerr@mail.mcgill.ca

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that are the norm for about 8 months of the year, and 2) a cold treatment that corresponds to temperatures that females and embryos experience during the coldest part of the annual cycle. Using the results of the laboratory experiment, I also re-examined field data on the dates of larval release across seasonal changes in temperature and inferred the timing of larval release relative to the diel cycle based on the time of the morning high tides.

Materials and Methods

Study System

The study area is located at the Pacific entrance to the Panama Canal in the Gulf of Panama, Central America. Tides are semidiurnal and of large amplitude (range = 2-6 m). The tidal amplitude cycle ranges in period length from 12-17 days. The spring high tides, the tides of large amplitude that occur during a 3-5-day period surrounding the maximum amplitude tide, usually occur between 4:00 and 7:00 a.m. and p.m. Sunrise and sunset occur at approximately 6:00-6:30 a.m. and p.m. in this tropical location. Water temperature in this area is typically 28-29°C and is constant during much of the year, but the Gulf of Panama experiences seasonal upwelling of cold, deep-source waters between the months of December and May, which decreases surface temperatures to approx. 20-25°C (D'Croz and O'Dea, 2007).

Uca deichmanni is a common species of fiddler crab found in the mid intertidal of low-energy sandy beaches in the tropical eastern Pacific from northern Costa Rica to northern Colombia. Females carry embryos on pleopods below their abdomen until they are ready to hatch. During incubation of the embryos, females spend the majority of their time in the sediment in closed burrows, but they are occasionally seen on the surface of the sand cleaning out the burrow and producing a mound of balls of sand (0.5-1 cm diameter), which they then use to cover the burrow entrance (Kerr et al., 2012). Burrows of ovigerous females were identified by the presence of this mound of sand balls covering a burrow entrance. Ovigerous females were collected from burrows at "Puente," a beach on the eastern side of the Panama Canal below the Bridge of the Americas (see Kerr et al., 2014b), during late afternoon low tides on 3 to 4 consecutive days for each of 3 runs of the laboratory experiment. Burrows of ovigerous females were identified by the presence of a mound of sand balls covering a burrow entrance.

Laboratory Experiment

To determine the effects of temperature on the timing of larval release relative to the tidal and diel cycles, I recorded the timing of larval release in two temperature treatments in the lab. Upon collection, ovigerous females were placed in plastic containers with sub-compartments, each with a few drops of seawater to keep the broods moist, and kept in a small cooler for transport to the Smithsonian Tropical Research Institute (STRI)'s Naos Marine Laboratories located on Naos Island, Amador Causeway, Panama City, Panama. Upon arrival to the lab, a small sample of eggs was taken from each brood for assessment of developmental stage and females were placed in aquaria as described below.

I observed eggs under a dissecting microscope and estimated the approximate percentage of yolk remaining. The majority of crabs started the experiment with broods of eggs containing high levels of yolk (average ± SE = 79.0 ± 3.13%, median = 90%, range = 25-100%), and carried out most of their development in the treatments. Incubation periods for crabs starting the experiment with broods with 90-100% yolk averaged 8.9 days (SD = 0.99 days) in the warm treatment and 12.4 days in the cold treatment (SD = 1.93 days). Each crab was individually labelled by affixing a numbered tag made of vinyl tape to her carapace with a tiny drop of cyanoacrylate glue.

Experiments were conducted during the wet (non-upwelling) season between June and August in 2010 in the outdoor seawater pavilion at Naos Laboratories. The pavillion is covered with a roof but is open on the sides, shielding the aquariums from rain, but providing natural light. For each water temperature treatment, a 190-liter insulated drum, receiving constant inflow from the laboratory seawater system, supplied water to the experimental aquariums through insulated PVC tubes. Ambient temperature in the seawater system pumped from the Bay of Panama was 28.9 ± 0.52°C (average ± SD) during the course of the experiments. For the cold treatment, water was chilled using a Tradewind 1/5 HP Drop-in chiller. Average temperature ± SD in the cold treatment aquariums was 23.0 ± 0.42°C. Small aquariums (30 cm × 30 cm × 20 cm) were randomly assigned to temperature treatments with three replicate aquariums for each temperature treatment (ambient or chilled). Aquariums were covered on all sides with black plastic and then insulated using 1.27-cm-thick polystyrene foam. Tops of aquariums were left open to expose females to ambient light but the air-water interface between the tubes that contained the females was insulated with polystyrene foam to minimize the effect of air temperature on water temperature. Aquariums were equipped with air stones and constant water flow. Females were randomly assigned to treatments and replicate aquariums and placed in PVC tubes (10 cm long × 3 cm inner diameter) with mesh on one end (Christy, 1982). The tubes were placed in the aquariums so that the females were approximately half covered by water. An additional tube containing an *iButton* temperature logger was placed in each aquarium in the same manner as those containing the females. *iButtons* measured water temperature every hour.

To determine when *U. deichmanni* females released larvae relative to the tidal and light/dark cycle, the females were checked for hatched larvae multiple times per day during three experimental runs. The time between consecutive checks on the females varied, so the time of each check and which females, if any, had released larvae was recorded. The time of release for each hatching event was estimated as the midpoint between the time when the release was recorded and the time of the previous check on the female. Precision of the estimated of time of release (the time period between consecutive checks) was determined for each release. Females whose hatching events were not recorded within a 3-hour time period were excluded from the analysis.

Timing of Release Relative to the Diel Cycle in the Field

Larval release relative to the biweekly tidal amplitude cycle across seasonal temperature variation in field enclosures was reported in Kerr et al. (2012). The dates of larval release by *U. deichmanni* for 278 individuals over 8 tidal amplitude cycles between 3 February and 15 April 2009 during upwelling and 21 May and 29 July 2009 during non-upwelling were recorded in that study. The present laboratory study inferred the time of release relative to the diel cycle for the Kerr et al. (2012) field data based on the time of the morning high tide on each day of release. These times of the morning (a.m.) high tides on the days when larvae were released (estimated times of larval release) were pooled for 3 tidal amplitude cycles during the non-upwelling season and 5 tidal amplitude cycles during the upwelling season. I used these times of the morning high tide, when females likely released larvae, to compare the timing of larval release relative to the light/dark cycle during the two seasons.

Data Analysis

Timing of release of larvae relative to the time of day was analyzed using circular statistical methods described in Zar (2010). Hatching times were categorized into hourly bins. For example, all releases that were estimated to have occurred between 6:00 and 6:59 were categorized as 6:00. Angles, or phase, for each hour of the day were determined by dividing 360° by 24 such that each hour of a day represents 15°. Binned hourly hatching times were converted to angles in degrees and plotted on circular plots using the GGplot2 package in R (Wickham, 2009) and subjected to descriptive and inferential statistics using the circular statistics package CircStat in Matlab (Berens, 2009). Mean angle (a) and resultant vector length or dispersion (R, range from 0 for randomly distributed to 1 for to identical values for all observations) are reported. To determine if release timing was significantly clustered, I used the omnibus or Hodges-Ajne test for uniformity of distribution and the v-test to test for deviation from a specified angle. The omnibus or Hodges-Ajne test (Zar, 2010) for circular uniformity provides a probability that the data come from a population with a uniform distribution of angles without the constraint of an underlying assumption of a unimodal distribution. A $p(o) < 0.05$ indicates that there is significant clustering of data. The v-test allowed me to test the alternative hypothesis that the data points are clustered around a mean angle not significantly different from 90° (6:00 a.m., approximate timing of sunrise). A significant result ($p(v) < 0.05$) indicates that the data are significantly clustered around a mean value not different from 90°, but a p-value > 0.05 could indicate that the data are uniformly distributed or that the mean angle is different from 90°. When the omnibus test is significant but the v-test is not, one can conclude that the releases are clustered but the timing is significantly different from that of 6:00 a.m. (around sunrise).

RESULTS

Laboratory Experiments

The times of 66 releases of larvae were recorded in the lab with a precision of 3 hours or less (time between consecutive checks on the females). Of all releases in both the warm and cold treatments 88% occurred during a time interval that included the high tide (Table 1). Only 2 larval releases occurred near the time of the low tide and the remaining 6 occurred during the ebbing tide. All *U. deichmanni* females kept in the warm treatment released their larvae during the high tide. The majority of these hatches (88%) occurred at night or near dawn (Table 1). Only 3 individuals in the warm treatment released larvae after sunrise. These all occurred during the high tide on days when the high tide occurred between 12:00 and 2:20 p.m. and were "early" rather than "late" relative to the day of the maximum amplitude tide (i.e., the tides were still increasing in amplitude rather than decreasing). One of these individuals carried eggs with only 25% yolk at the beginning of the experiment but the other two carried broods with 80% yolk when collected and released larvae after a short incubation period relative to the other females in the same treatment. Of the 42 releases of larvae in the cold treatment, 81% occurred during high tide, 4 of which were at night, 20 at dawn and 10 during the day. All larval releases that occurred after high tide (19%) were by females in the cold treatment on days when the morning high tide occurred during daylight. Of all females in the cold treatment (all tidal states), 33% released larvae at least one hour after sunrise and 57% released at dawn. Since sunrise occurred between 5:58 and 6:10 a.m. during the experiments but releases that occurred between 6:00 and 6:59 were categorized as 6:00 a.m., 9 of the larval releases categorized as 6:00 a.m. actually occurred just after sunrise. When these releases are included, 55% of females released larvae after sunrise in the cold treatment.

Using the hourly bins of estimated times of release, I employed circular statistics to calculate the average time of day of hatching and the dispersion or synchrony of hatching times. Under ambient, warm conditions the average timing of release was between 4:00 and 5:00 a.m., while in chilled conditions the average release occurred at approximately 7:00 a.m. (Fig. 1). In both temperature treatments, the time of release was highly clustered ($p(o) < 0.001$) and was not significantly different from the time of sunrise, which ranged from 5:58 to 6:10 a.m. during the study (approx. 90°, $p(v) < 0.001$). The majority of releases therefore occurred during the large amplitude high tides that occurred within a couple of hours of the time of sunrise. Of particular note is the fact that *U. deichmanni* females always released larvae during the morning high tide, even when hatching occurred on days when the high tides were at dawn and dusk or shortly thereafter, rather than switching to the high tide at dusk or early evening (Fig. 1).

Timing of Release in the Field

The average timing of larval release in the field enclosures during 3 tidal amplitude cycles of the non-upwelling (warm) season occurred 2-3 days before the maximum amplitude tide (Kerr et al., 2012). Assuming that females released their larvae during the morning rather than evening high tides in the field, as they did in the lab, I estimated the time of larval release to be the time of the morning high tide on the days of release. The time of the high tide on the mean day of larval release across the pooled 3 tidal amplitude cycles was about 4:00 a.m. (Fig. 2). During these three cycles only a few individuals released larvae on days when the morning high tide happened at or just after sunrise (0-22% per cycle, high tide occurred at 7:51 a.m. on the day of the latest release, Fig. 2), but the majority of releases would have occurred during darkness.

In contrast, the time of the morning high tide on the average day of release was 5:30 a.m. during the upwelling season (Fig. 2). Of all releases recorded during the upwelling season (5 tidal amplitude cycles) 65% occurred on days when the high tide occurred at night or just before dawn and another 7% released on days when the high tide occurred within a half hour of sunrise (Fig. 2). Nonetheless, the average days of release when only the 3 coldest tidal amplitude cycles are considered, had morning high tides that occurred after sunrise (6:40 to 7:40 a.m.), and 47 to 81% of all releases for these cycles occurred on a day when the morning high tide was after sunrise. The latest release occurred on a day when the morning high tide was at 11:19 a.m. (Fig. 2).

DISCUSSION

This study establishes that *U. deichmanni* releases larvae mainly during nocturnal, spring, high tides. This timing is the most common pattern (83%) for the 36 species of intertidal crabs for which data are available for all 3 environmental cycles (diel, tidal, tidal amplitude) (Christy, 2011, supplementary table). *Uca deichmanni* continued to release larvae during the morning high tides even when the period of incubation increased by several days in the cold-water treatment and the morning high tide occurred after sunrise. Some species, including *Uca terpsichores* Crane, 1941, a species of fiddler crab that is closely related to, and often lives on the same beaches as *U. deichmanni*,

Table 1. Number of females of the fiddler crab *Uca deichmanni* releasing larvae during each tidal and diel state in ambient (approx. 29°C) and cold (approx. 23°C) temperature treatments in the laboratory. Crabs with broods of all yolk stages at the beginning of the experiment (25-100%) were included in the analysis but the majority of crabs started the experiment with eggs containing high levels of yolk remaining (median = 90% yolk).

Treatment	*N*	Tidal State				Diel State			
		High	Ebb	Low	Flood	Dusk	Night	Dawn	Day
Ambient	24	24	0	0	0	0	12	9	3
Cold	42	34	6	2	0	0	4	24	14

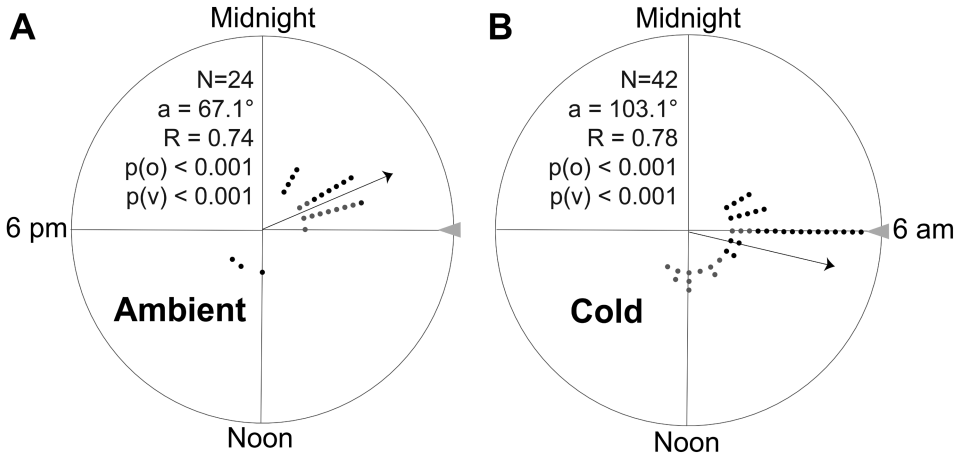

Fig. 1. *Uca deichmanni* larval release in the lab. Time of day of the release of larvae by ovigerous fiddler crabs *U. deichmanni* in ambient (29°C) and cold (23°C) temperature treatments in the laboratory. The grey arrow indicates the approximate time of sunrise (approx. 6:00 a.m.) during the experiments. Crabs with broods of all yolk stages (25-100%) were included in this analysis but the majority of crabs started the experiment with eggs containing high quantities of yolk (median = 90% yolk). Releases by crabs beginning the experiment with 100% yolk are indicated by gray dots (10 ambient, 13 cold) while black dots represent releases by females that began the experiment with broods containing all other yolk quantities. Times of the high tides were categorized into hourly bins prior to analysis (ex: tides from 5:00 to 5:59 were categorized as 5:00). Sample sizes (N), summary statistics (a, mean angle; R, resultant vector length) and *p*-values for the omnibus test (o) and v-test (v) are shown for each temperature treatment.

maintain the timing of larval release during darkness by switching from the morning to the evening high tide when the morning tide occurs after sunrise (Christy, 2003; Christy and Backwell, unpublished data). Other crabs that live in colder water and have low synchrony of larval release among individuals also release during either evening or morning high tides, thus maintaining release during darkness or twilight for the most part (Rasmuson et al., 2014). A few other species do release larvae, at least partially, during the day. Yamaguchi (2001) found that 40 to 60% of *Uca lactea* (De Haan, 1835) females released their larvae near the time of high tides that occurred during daylight. Morgan and Christy (1995) reported that *Uca beebei* Crane, 1941 releases larvae during the higher high tide of each 24-hour period even though those tides often occurred during the day. Based on experiments of predation on larvae of differing coloration and their patterns in the timing of larval release, they concluded that *U. beebei* larvae may be more protected than other crab larvae due to their coloration and the habitat in which they are released (Morgan and Christy, 1997). *Uca thayeri* Rathbun, 1900 releases larvae during the night-time large or maximum amplitude high tides where tides are semidiurnal, but releases larvae during daytime large or maximum amplitude high tides in a mixed tidal regime where larger amplitude tides do not occur at night (Kellmeyer and Salmon, 2001; Weaver and Salmon, 2002;

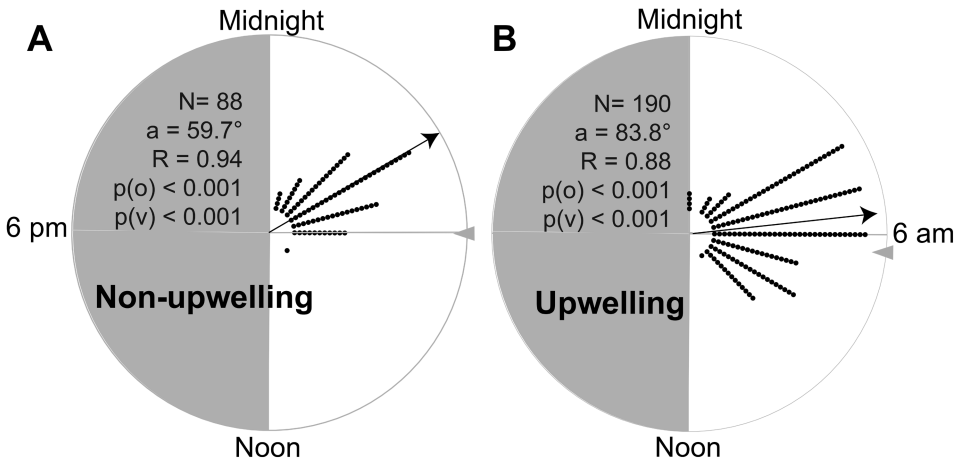

Fig. 2. *Uca deichmanni* estimated timing of larval release in the field. Time of day of the morning high tide on days when ovigerous *U. deichmanni* fiddler crabs released larvae in field enclosures during non-upwelling (average sediment temperature = 28.8°C) and upwelling (24.2°C) conditions. Data are from 3 tidal amplitude cycles during the non-upwelling season (23 May to 29 July 2009) and 5 tidal amplitude cycles during upwelling (3 February to 15 April 2009). The grey arrow on the outer margin of the circle indicates the approximate time of sunrise during data collection for that season (non-upwelling: 5:58-6:08 a.m., upwelling: 6:09-6:39 a.m.). Times of the high tides were categorized into hourly bins prior to analysis (ex: tides from 5:00 to 5:59 were categorized as 5:00). Since releases were assumed to have occurred during the morning high tides, afternoon and evening high tides were excluded and those time periods have been shaded in gray in the plots. Sample sizes (N), summary statistics (a, mean angle; R, resultant vector length) and *p*-values for the omnibus test (o) and v-test (v) are shown for each temperature treatment.

Christopher et al., 2008). Christy (2011, supplementary table) compiled 8 additional reports of intertidal crabs releasing during the day out of 64 for which the diel period was reported. For all of these instances where crabs release larvae during the day, the crabs also release larvae at night.

This preference, or constraint, by *U. deichmanni* from switching to the evening tide may have detrimental effects on the survival of newly hatched larvae since experiments have shown that risk of planktonic predation is higher during the day than at night (Kerr et al., 2014a). In Panama, dusk was the safest time period overall for tethered plankton and risk was highest during the daytime for small plankton (Kerr et al., in press). Furthermore, risk of predation on small plankton was higher during the upwelling season than during non-upwelling (Kerr et al., in press). Switching the timing of release of larvae to the evening tide, especially during upwelling when predation risk is higher and errors in timing are more likely, should therefore result in increased survival of larvae.

While the diel cycle is important for the timing of larval release of many species, tidal amplitude and tidal height also play roles, especially if there are constraints on releasing larvae during large amplitude high tides at night (Kellmeyer and Salmon, 2001; Yamaguchi, 2001; Christopher et al., 2008; Christy, 2011). Larger amplitude tides result in stronger tidal currents and increased potential of movement of larvae offshore during subsequent ebb tides. Higher high tides cover more of the intertidal habitat and allow females in the upper intertidal to release larvae from the safety of their shelters. Of the two high tides per day that occur in semidiurnal areas, the high tide with higher height often also has a larger amplitude. This is not always the case though. High tides on the Pacific coast of Panama occur near the time of sunrise and sunset on two days of each semi-lunar tidal amplitude cycle. On these days, neither high tide occurs during complete darkness. During this study, sunrise high tides were slightly higher in height, but were smaller in amplitude, than high tides occurring at sunset. On all other days of the tidal amplitude cycle, high tides during daylight, including those just after sunrise, were of both larger amplitude and higher height than the high tides occurring during darkness. Therefore, larvae released during tides before dawn were released under the cover of darkness, but were released during tides with smaller tidal amplitude and height than the afternoon tide, and they had little time to move offshore before daylight. In contrast, post-sunrise releases of larvae had the advantage of larger amplitudes and higher heights of the tide relative to post-sunset releases, although the absolute amplitudes and heights on these days were lower than those occurring just before sunrise and sunset. Thus, when *U. deichmanni* females are forced to release larvae later in the tidal amplitude cycle due to the effects of temperature on development of embryos, the larger amplitude of these daylight high tides relative to the evening tides may somewhat diminish the risk of predation during daylight by sweeping the larvae away from shore and the higher densities of predators.

Uca deichmanni targets the release of larvae during high tides that occur just before dawn during ambient, warm conditions. The timing of the maximum amplitude tide ranges from ~4:00 a.m. to 7:00 a.m. throughout the year. The maximum amplitude high tides during the three tidal amplitude cycles of the experiments occurred at 5:06, 5:08 and 5:20 a.m. Larval release in the ambient treatments was therefore very well timed with a maximum amplitude high tide that occurred during the cover of darkness. This near-dawn timing, however, leaves little leeway for error and means that temperature-induced increases in incubation period of only a day or two may result in larvae being released during daylight. Kerr et al. (2012) found that the average day of larval release in the field during warm conditions was 1-3 days before the maximum amplitude tide and was 1-2 days after the maximum amplitude tide during the coldest conditions. Re-examination of this data, with the consideration that *U. deichmanni* does not switch to the afternoon/early evening high tides that occur after sunset, revealed that during the coldest conditions, the average timing of larval release corresponded with tides that occurred just after sunrise and that a large proportion of releases would have occurred during daylight. The proportion of individuals that released larvae during daylight in cold conditions was, however, quite a bit lower in the field (36%) than in the lab (55%).

The reason that *U. deichmanni* does not switch to the evening tide while other species do remains unknown. Increased risk of predation associated with larval release during the day, and higher predation risk overall during upwelling when these crabs are most likely to release larvae late (Kerr et al., 2012, 2014a, in press), may provide strong selection for targeting the largest amplitude tides that occur before dawn, or releasing larvae during darkness on slightly lower amplitude tides, as does *U. terpsichores*. Kerr et al. (2014b) showed that *Uca terpsichores* adjust to changes in temperature and reduce the magnitude of potential errors in timing of hatching by changing the timing of courtship. In contrast, *U. deichmanni* does not shift timing of courtship (Kerr et al., 2014b). Despite this, during cold conditions in the field, *U. deichmanni* released larvae more synchronously and closer to the maximum amplitude tides than did *U. terpsichores* (Kerr et al., 2012). Differences in timing between the lab and the field, high synchrony and relatively low rate of errors in timing of release indicate that *U. deichmanni* may use some method of adjustment to decrease the magnitude of timing errors (Kerr et al., 2012). One possibility is the regulation of incubation temperature via movements within their burrows. Release of larvae among female *U. terpsichores* is of relatively low synchrony but a switch to releasing during the evening tide when the morning tide occurs after sunrise may afford them some respite from potential risk of predation associated with errors in timing. In contrast, errors in timing by *U. deichmanni*, while rare, result in releases of larvae that occur during daylight and may prove costly in terms of larval survival, potentially increasing selection to hit the targeted timing. In other words, the penalty, in terms of fitness, for missing the targeted timing may be larger in for *U. deichmanni* than for *U. terpsichores*. On the other hand, the higher synchrony of releases by this species may mean that the need to switch to the evening tide may be relatively low. The coldest conditions that resulted in relatively high proportions of daytime releases of larvae in the field occur during only

a few of the approximately 8 biweekly tidal amplitude cycles that occur during an upwelling season. Errors in timing induced by temperature variation may prove quite costly during a small number of reproductive bouts per year, potentially resulting in reduced recruitment for a few tidal amplitude cycles, and affecting the size of these population cohorts. Nonetheless, the low frequency of these events, in the context of a species that reproduces up to 26 times per year, may limit the overall impact of these errors on the population. The large scale effects of errors in timing of larval release have yet to be determined.

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