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Seaward Migration and Larval Release Coincide with Lunar and Light-dark Cycles in Supratidal Land Crabs *Cardisoma carnifex* and *Epigrapsus notatus*

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Herein we investigated the synchronous breeding migration and larval release of ovigerous females in two dominant supratidal land crabs *Cardisoma carnifex* and *Epigrapsus notatus* in the mixed semidiurnal tidal regime in Taijiang National Park (Tainan, Taiwan). We mainly focused on the monthly and daily rhythms during the breeding season of migration and larval release for these two crabs. We also sought to understand what the main environmental cues were for these monthly and diel rhythms. Both lunar and tidal amplitude cycles are potential proximate causes for the monthly lunar/semilunar reproductive rhythm in crabs. Likewise, either the 24-hour (diel) light cycle or tidal cycle can act as the proximate cause for diel reproduction rhythm, and we investigated which one was the main factor that entrains the diel rhythm for these two species. We found that the season of migration and larval release in *C. carnifex* occured mainly between June and September during the rainy season while those of *E. notatus* occurred mainly between September and October, near the end of the rainy season. Regarding the rhythm of migration and larval release in monthly time scale, *C. carnifex* exhibited a semilunar rhythm following the syzygies and *E. notatus* exhibited a lunar rhythm following the full moon. However, these rhythms did not occur with the maximum amplitude nocturnal and diurnal high tides. This implies that the lunar cycle is a more important environmental cue than the tidal amplitude in the entrainment of the synchronous monthly breeding rhythm for these two species. This pattern is different from other intertidal crabs, most of which use the tidal amplitude cycle as the main environmental cue for larval release. In addition to *Chiromantes haematocheir* (a supratidal crab), our study provided two more species that live in the supratidal zone time their reproduction with respect to the lunar light cycle and independent of the tide amplitude cycles. For the diel rhythm, both species migrated to the shore and released larvae in the first half of the night during the flood tide. This suggests that the diel light cycle is a dominant cue for the determination of larval release timing for these two species. Larval release does not track the high slack tides, since larvae are only released during the first half of the night and these high slack tides occur only after midnight (0000–0600H) during the days of larval release for these two crab species.

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Key words: Breeding migration, Larval release, Mixed semidiurnal tides, Supratidal land crabs, Semilunar rhythm.

BACKGROUND

The gecarcinids (the family Gecarcinidae) are a group of "land crabs" inhabiting islands and continental maritime forests of supratidal (above the high tide level) areas in the tropics and subtropics. Although gecarcinid crabs spend most of their juvenile and adult lives in terrestrial habitats, their larvae need saline water to hatch and develop (Cuesta et al. 2002; Hartnoll 1988; Wolcott 1988). Therefore, ovigerous females must migrate to the sea shores from their resident terrestrial habitats to release larvae.

A striking phenomenon in the gecarcinids is that the female crabs perform synchronized seaward migration for larval release (Hicks 1985; Johnson 1965). Such synchronized reproductive activities have been studied for species including *Cardisoma guanhumi* (Henning 1975); *C. hirtipes* (Shokita 1971); *Epigrapsus notatus* (Liu and Jeng 2005); *E. politus* (Doi et al. 2020); *Gecarcinus lateralis* (Bliss et al. 1978); *G. ruricola* (Hartnoll et al. 2007); *Gecarcoidea lalandii* (Liu and Jeng 2007); *G. natalis* (Adamczewska and Morris 2001; Hicks 1985); and *Johngarthia lagostoma* (Hartnoll et al. 2006). The reproductive synchrony in these land crabs does not occur randomly, but rather is precisely timed and exhibits several types of rhythm in different temporal scales including annual rhythm (yearly time scale), semilunar and lunar rhythm (monthly time scale), and diel (24-hour) and tidal rhythm (both belonging to daily time scale). The rhythmic synchronous reproduction is important for settlement and metamorphosis of the larvae on suitable substrates (Christy 1978; Morgan and Christy 1995; Wheeler 1978).

The reproductive synchrony in the intertidal and supratidal brachyurans appears to be endogenous and entrained to a variety of environmental factors (the proximate causes) (Christy 2011; Dennenmoser et al. 2020; Forward 1987; Morgan and Christy 1995). On a monthly time scale, these crabs exhibit either a lunar or semilunar rhythm in their breeding migration and larval release depending on the species and the habitat where they are found (Christy 2011; Forward 1987; Wolcott and Wolcott 1982). The most common pattern is that breeding migration and larval release often occur when the nocturnal ebb tides reach their greatest amplitudes, usually corresponding to the spring tides near the days of new and/or full moon (Christy 2011). The proximate causes of semilunar/lunar breeding rhythm have long been attributed to the fluctuations in either the tidal amplitude (biweekly cycle of daily differences between the height of high and low tides, synonymous with the spring-neap cycle) (Christy 2011; Dennenmoser et al. 2020; Morgan 1996a; Morgan and Christy 1995) or the moonlight (Saigusa 1980 1988). However, to determine which of these two environmental cues is more consequential is not an easy task, because tidal amplitude cycles are usually highly correlated with lunar cycles in most locations (Barnwell 1976). Likewise, the diel rhythm of breeding migration and larval release may depend upon the interaction of light-dark cycles and semidiurnal or diurnal cycles of high and low tides (Forward 1987). The most common pattern is that these crabs migrate to the estuarine shores to release larvae after dusk around the time of high tide (Christy 2011; Forward 1987). However, daily high tides near dusk occur in some coastal areas (Saigusa 1982), making it difficult to distinguish whether the diel rhythm of larval release coincides with the light-dark or tidal cycle. The exhibition of the specific rhythms in monthly and diel time scales may facilitate the rapid transportation of larvae offshore by strong ebb tides (Morgan and Christy 1995), increasing the survival of newly hatched larvae by decreasing their risk of predation by planktivorous fishes (Morgan 1989 1990). It may also reduce the physiological stress of larvae from low salinity due to their low tolerance to low salinity water (Forward et al. 1982; Saigusa 1981). Because the survival and transport of early-stage larvae by currents are determined by the spatiotemporal patterns of larval release (Christy 2011; Dennenmoser et al. 2020) and the expansion of geographical distribution and metapopulation network of land crabs is determined by the transport of larvae (Anger 2006), it is important to characterize the dynamics of larval release by land crabs to understand future population structure.

We conducted our study at the Chengxi windbreaks in Taijiang National Park (Taijiang hereafter), which provided a suitable place to study the reproductive biology of *Cardisoma carnifex* and *Epigrapsus notatus* (Fig. 1). Taijiang National Park is a wetland park located on the southwest coast of Taiwan. The Chengxi windbreaks are the most important land crab hotspots in Taijiang, with a huge variety of land crab species and vast numbers. There are currently 32 species in six families of land crabs in the park (about 85% of the overall species of land crabs) are recorded (Liu 2021). Within these crabs, *Cardisoma carnifex*, *Epigrapsus* *notatus*, *Helice formosensis*, *Parasesarma bidens*, *Ocypode ceratophthalma* and *O. sinensis* are the dominant species (Liu 2020 2021). *Cardisoma carnifex* is the most common land crab in terms of its large size, wide distribution, and vast numbers. *Cardisoma carnifex* burrow in a variety of muddy habitats including the coastal windbreak forests, mangrove swamps, coastal shrubs, and even the walls of fish ponds (Liu 2021). *Cardisoma carnifex* can be found to inhabit damp environments as far as five kilometers from the sea in Taijiang (Liu 2021). The population size of *C. carnifex* in the park is considered to be the largest in Taiwan (Liu 2021). *Epigrapsus notatus* is the second most abundant gecarcinid in Taijiang. This species is only distributed in the belt-type Chengxi windbreaks from the coastal border of Zengwen estuary to Luermen River in Taijiang (Fig. 1) (Liu 2021). Thus, the populations of both *C. carnifex* and *E. notatus* are adequate for reproductive biological research.

Taijiang National Park also provides a suitable

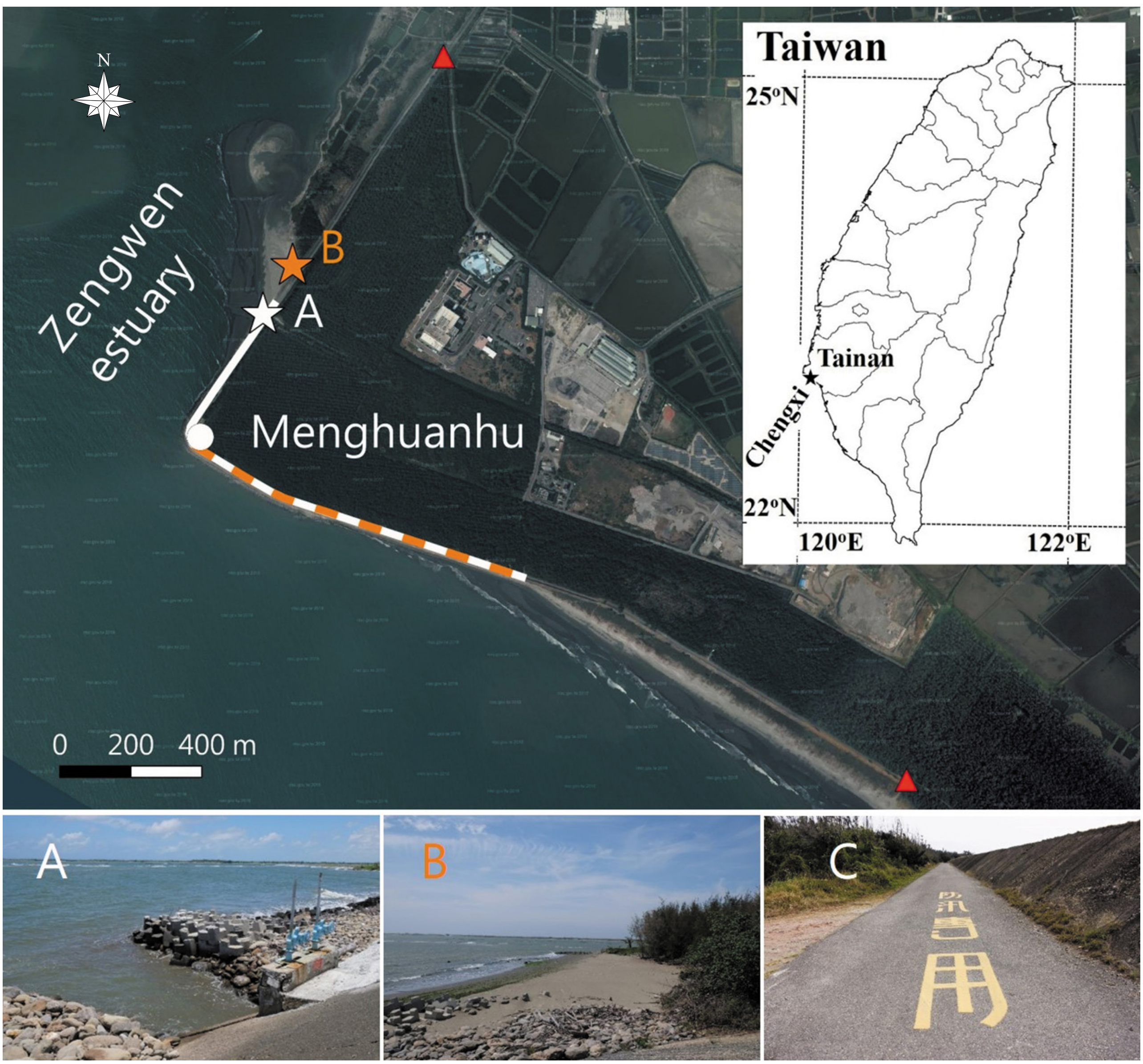

Fig. 1. The location of the study area of the crabs in Chengxi windbreaks of Taijiang National Park, Tainan, Taiwan. Red arrows indicate the start point and end point of the migration survey on the road in 2020. The white line (1450 m) and orange line (950 m) represent the migration survey areas on the embankment flood control road for *Cardisoma carnifex* and *Epigrapsus notatus*, respectively, in 2021. The white asterisk (site A, photograph A) and orange asterisk (site B, photograph B) represent the sites for the observation of larval release of *C. carnifex* and *E. notatus*, respectively, in 2021. Photograph C is the embankment flood control road where the surveys of crabs took place.

place to study the possible proximate causes that entrain the reproduction rhythms of land crabs. The tidal regime in Taijiang belongs to the mixed semidiurnal tides (usually two, but sometimes one tidal cycle per day) (Liu 1996; Tsai 2010). However, due to the latitude as well as the geometry and depth of the seafloor in southwestern Taiwan (Liu 1996; Tsai 2010), the maximum amplitude nocturnal and diurnal high tides do not coincide with the new and full moons but rather with quarter moons from June to October (Figs. 2 and 3), the potential migration and larval release season for these two crabs. Moreover, all the daily nocturnal high tides in Taijiang occur in the second half of the night following the days of new and full moons (https://www.cwb.gov.tw/) (Liu 1996) for about one week during the season for migration and larval release in these two crabs. As the timing of maximum amplitude high tides are shifted from the syzygies and the timing of daily high tides are shifted from the dusk (the time when migration and larval release usually occurs) in Taijiang, a good opportunity is provided to determine which of the environmental factors (*i.e.*, lunar cycle vs tidal amplitude) are the main exogenous cues that entrain the lunar/semilunar rhythms and diel rhythms in these two crabs by comparing the variation in the timing of migration and larval release (the expression of plastic traits) relative to these environmental cycles (Morgan 1996a; Morgan and Christy 1994).

Our study had two goals. Our first goal was to investigate the timing of breeding migration and larval release of two gecarcinids *C. carnifex* and *E. notatus* that occur supratidally in the coastal forests (the Chengxi windbreaks) in Taijiang National Park. We mainly focused on the breeding season and the population rhythm in migration and larval release in terms of the monthly time scale (*i.e.*, the lunar and semilunar rhythm) and the daily time scale (*i.e.*, the diel rhythm) in these two crabs. The second goal was to understand what the main environmental cues for the monthly and diel rhythms in these two crabs are. Because the timing of larval release is important for reproductive success, crabs may adopt different mechanisms to regulate the timing of breeding depending on where adults live and the physical cycles they experience (Christy 2011; Morgan and Christy 1995). Fluctuations in the tidal cycles and tidal amplitudes could easily be sensed by intertidal and subtidal crabs, and thus these crabs typically use these cues to entrain their breeding rhythm. However, it may not work for supratidal crabs because their habitats are not inundated by the tides. Thus, the supratidal crabs may use other cues as environmental stimuli for breeding rhythms, *e.g.*, the lunar cycle or the light-dark cycle (Saigusa 1980 1988 1982). Therefore, we hypothesized that the lunar cycle and the light-dark cycle may act as the proximate cause for lunar/semilunar and diel rhythms, respectively, in these two crab species. By synchronizing their endogenous rhythms with these environmental cues, these crabs can anticipate and reliably time their reproduction to fulfill one of the most important activities in their life.

MATERIALS AND METHODS

Study area and a brief description of the experimental design

This study was conducted around the Chengxi windbreaks (23°02'31"N, 120°04'03"E) in Taijiang National Park, Tainan, Taiwan (Fig. 1). The windbreaks were planted for wind-breaking and sand-binding on the tidal flats of Zengwen River. There is an embankment flood control road in the Chengxi windbreaks that crabs must cross over to get to the sea during their breeding migration (Yuan Mou Chang, personal observation) (Ding et al. 2017). Thus, this road provides a means to monitor, observe, and study the daily and seasonal rhythms of the breeding migration of *C. carnifex* and *E. notatus*.

The study site is located south of the Tropic of Cancer, in the subtropical zone with a Monsoon and Trade-wind Coastal Climate (Am) and an average annual temperature of 24°C. The rainy season in Tainan falls between May and September due to weather frontal systems, and typhoons bring heavy rain during these months. The rainy season corresponds to about 80% of the annual precipitation. Rain is rare after September (Chen et al. 2018; Lee 2005). The location experiences mixed semidiurnal tides (Liu 1996; Tsai 2010).

There were two stages in this study. The first stage took place between March and November 2020 and involved gathering data on the season and rhythm of breeding migration of *C. carnifex* and *E. notatus*. The second stage took place between June and November 2021, and again involved investigating the dynamics of breeding migration but also involved gathering data on the timing of larval release of these two crabs.

Stage 1: Breeding season, dynamics of breeding migration and body size measurement

In this stage, monthly variations in the numbers of crabs crossing a section of 4 km on the embankment flood control road were collected from March to November 2020 (Fig. 1). Because these two crab species only move during the nighttime hours, surveys were conducted between 1800H and 2400H on a couple of days before and after the new moon and full moon and during other lunar periods (120 days in total; 4 d in March, 5 d in April, 7 d in May, 12 d in June, 20 d in July, 17 d in August, 17 d in September, 21 d in October and 17 d in November). To conduct the survey, we rode a motorcycle back and forth during this period along this section of the coastal road. Whenever we saw a crab, we stopped and recorded the date and sex. We then drew a line on the dorsal surface of the carapace with a white oil-based marking pen to prevent us from sampling the crab more than once and released the crab

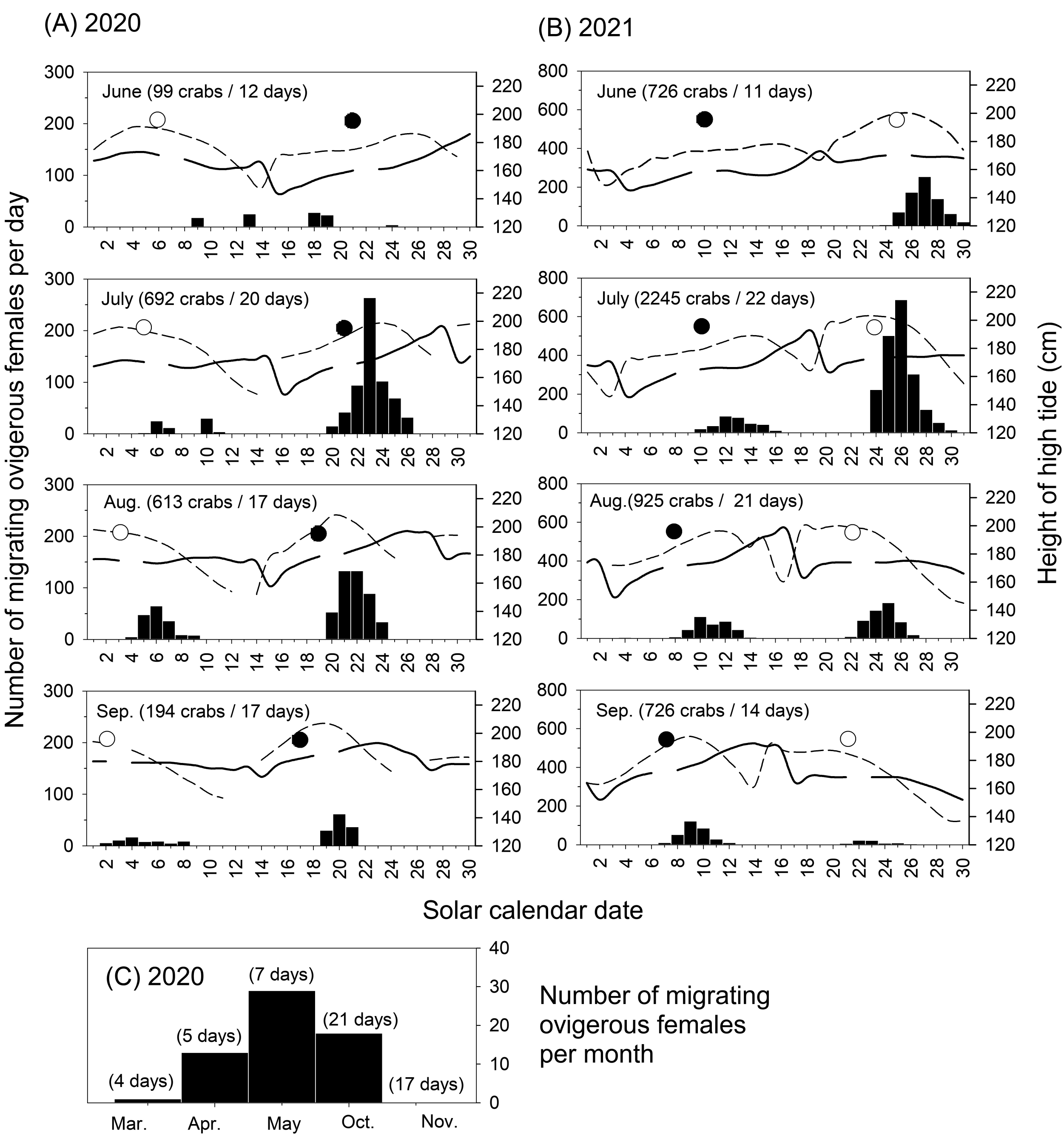

Fig. 2. Temporal pattern of migrating ovigerous female *Cardisoma carnifex* recorded on the embankment flood control road of Chengxi windbreaks between March and November 2020 (A, C) and between June and September 2021 (B). Solid lines (—) and dash lines (---) represent nocturnal (1800-0559H) and diurnal (0600-1759H) high tides, respectively. The breaks in the lines indicate a lack of data on tidal height for the observation days. Closed and open circles represent new and full moons, respectively. Because few *Cardisoma carnifex* were found on the road in March, April, May, October and November ($n < 30$), the numbers of female crabs per month were combined (C).

unharmed onto the road.

Stage 2

Dynamics of breeding migration and body size measurement of ovigerous females

In this stage, we narrowed our survey area to a section of the embankment flood control road near Menghuanhu ("Dream Pond") because our 2020 surveys (Fig. 1) showed this area to have a higher concentration of individuals than the other areas in the survey. We also conducted the survey from June to November in 2021, since the 2020 results showed that *C. carnifex* begin their breeding migration in June. The length of road surveyed was 1450 m for *C. carnifex* and 950 m for *E. notatus*. Surveys were conducted nightly for the seven days following the new moon and the seven days following the full moon (24–30 June, 22–28 August, 7–13 September, 21–29 September, 22–28 October and 22–25 November). In addition to these, the surveys were also conducted nightly from July 10 to August 14. Three people executed the survey for *C. carnifex* due to vast numbers and two people did the same for *E. notatus* at the same time.

We began each survey at 1900H (well after the sunset) and continued until no ovigerous females were seen for a period of 1 hour, since the 2020 surveys found that most crabs migrated to the shore between sunset and midnight. Again, surveys were accomplished by looking for ovigerous female *C. carnifex* while riding a motorcycle and/or walking along the target section of the coast road. We only focused on ovigerous female *C. carnifex* since male *C. carnifex* were rare on the road, not involved in the breeding migration, and never found on the shore during the 2020 surveys (stage 1). When an ovigerous female *C. carnifex* was encountered, we recorded the same measurements described above, marked their carapace, and then released the crab. Ovigerous female *E. notatus* were also caught and recorded as above, but identification numbers (ID) were applied to the dorsal surface of the carapace with a white oil-based marker. These individuals were subsequently put into a plastic aquarium (25 × 10 × 10 cm) and transported to site B as soon as possible for the observation of the timing of larval release (see below).

Larval release timing

We observed the timing of larval release for ovigerous *C. carnifex* at the opening of a man-made water channel on the seaward side of the embankment connected to the mouth of Zengwen estuary (site A, Fig. 1) and, for ovigerous *E. notatus*, on a sandy beach near site A (site B, Fig. 1). There were rocks and wave dissipating concrete blocks lining both sides of the channel. We selected the opening for observation because it is a main spot for larval release of ovigerous *C. carnifex*. The observations of *C. carnifex* were performed during the week beginning with the new moon and the week beginning with the full moon (*i.e.*, 24–30 June, 10–15 July, 24–30 July, 8–14 August, 22–28 August, 7–13 September, 21–29 September 2021). The observation started at 1900H and then proceeded until no ovigerous females were seen for 1 hour. We caught ovigerous *C. carnifex* approaching the opening and marked them with identification numbers on the carapace using a white oil-based marker, and then released them at the point of capture. While we remained at or near the channel opening, we constantly inspected the marked females by using flashlights. We recorded the timing of larval release by spotting the back-and-forth fanning behavior of their bodies under water, which is an indicative behavior for this event (Cheng 2012).

The observations of *E. notatus* were performed for a week, beginning on the third day after a full moon, *i.e.*, 23–29 September and 22–28 October 2021. The small size and fewer numbers of *E. notatus* made observation of larval release difficult among the wave dissipating concrete blocks outside the shoreline embankment during the dark of night. Consequently, The method of determining the timing of larval release of *E. notatus* is somewhat different from that of *C. carnifex*. Captured ovigerous females were delivered from the road to site B, where they were gently transferred to and maintained in a plastic box (40 × 30 × 21 cm) set on the sandy beach (Christy 1986). The box was tilted on the beach so that only two-thirds of the bottom was covered by seawater. Thus, female crabs could stay above water before they moved into the water to release their larvae. We checked the crabs every 5–10 minutes using flashlights. The timing of larval release was determined by observing the females entering the water and shaking their bodies (Liu and Jeng 2005) or the actual release of larvae. Once the females released their larvae, we removed them from the box and returned them to the embankment flood control road on the side of the windbreaks.

Meteorological information

To understand whether the timing of larval release for these two gecarcinid crabs correlates with the nighttime tidal amplitude cycle and high tides, tidal data were obtained from the weather station at Jiangjun (23°12'45"N, 120°04'59"E) about 18 km north of the study area (https://www.cwb.gov.tw/V8/C/M/

tide.html?NSeaID=NSea06). Nighttime in this paper is defined as the time interval between the time after sunset (about 1900H) and before sunrise (about 0500H). The daily nighttime tidal amplitude is defined as the range of height between the high tide and low tide each day. When the low tide occurred during daylight, the one closest to 0600H or 1800H was designated as the nocturnal low tide for that day.

Data analysis

We collected data between June and September and between September and October of 2020 and 2021 for *C. carnifex* and *E. notatus*, respectively. This was during the main breeding migration season of these two species. We used a Rayleigh's test (Zar 1999) calculated in Microsoft Excel (version 2013, Microsoft) to determine whether intervals of seaward migration were correlated with the lunar cycle (or semilunar cycle) and the tidal amplitude cycle; whether the timing of release of ovigerous females were correlated with the lunar cycle (or semilunar cycle), tidal amplitude cycle, tidal cycle, and light-dark cycle. Circular distribution of the intervals of seaward migration and the timing of larval release with environmental cycles (*i.e.*, lunar cycle, tidal amplitude cycle, tidal cycle, and light-dark cycle) were used. The first step of the test was to calculate the magnitude of the r-value. This value, a measure of the temporal concentration of release times, is used to indicate whether the timing of larval release is uniform during a particular cycle. The r value is between zero and one. A higher r-value represents a less uniform, more concentrated timing of the release of larvae, indicating that the larval release timing is more consistent with a particular environmental cycle. If the r value was significantly high, the mean angle and angular deviation (standard deviation) of each distribution were calculated to identify peak time and their dispersion of seaward migration and larval release. Data are expressed as means ± 1 SE.

RESULTS

Breeding season and the rhythms of breeding migration

C. carnifex

A total of 1521 and 4253 ovigerous female *C. carnifex* were observed migrating to the sea in 2020 and 2021, respectively. The majority of the migration occurred between June and September, the onset of the rainy season and the end of the rainy season, respectively (Fig. 2). The main migration season was July and August (Fig. 2A, 2B), and the number of migrating females decreased abruptly in October (Fig. 2C).

The migration exhibited a semilunar rhythm. The peak migration occurred about 3 days after the new and full moon (3.3 ± 2.6 days in 2020; 3.2 ± 1.3 days in 2021) during the intermediate amplitude nocturnal high tides (5.6 ± 6.6 days before and 8.9 ± 7.1 days after the maximum amplitude nocturnal high tides in 2020 and 2021, respectively) (Table 1; Fig. 2A, 2B). The migration seemed to occur around the maximum amplitude diurnal high tides (1.0 ± 11.0 days and 2.8 ± 8.6 days after the maximum amplitude diurnal high tides in 2020 and 2021, respectively), but with r values of 0.42 and 0.50 in 2020 and 2021, respectively (Table 1; Fig. 2A, 2B). This suggests that the timing of migration was less consistent with the maximum amplitude diurnal high tides. The daily number of seaward migrating females varied with the lunar phase. The highest number of daily migrating females was 264 and 687 crabs occurring on 23 July 2020 and 26 July 2021, respectively (Fig. 2A, 2B).

E. notatus

A total of 107 and 207 ovigerous female *E. notatus* were observed migrating to the sea in 2020 and 2021, respectively (Fig. 3). The majority of the migration occurred at the onset of the dry season with a major movement of ovigerous females in late September and late October, but a minor movement in late November (Fig. 3).

The migration exhibited a lunar rhythm. The peak migration occurred about 20 days after the new moon (20.5 ± 1.3 days in 2020; 20.0 ± 1.3 days in 2021) during the intermediate amplitude diurnal/nocturnal high tides (Table 1; Fig. 3A, 3B) and lasted for about one week. Based on the data collected in 2021, about one and a half times as many females migrated in late September (n = 124) than in October (n = 80) (Fig. 3B). The daily number of seaward migrating females varied with the lunar age. The highest number of daily migrating females was 27 and 39 crabs occurring on 7 October 2020 and 26 September 2021, respectively (Fig. 3A, 3B).

Timing of larval release

C. carnifex

Similar to the migration rhythmicity of ovigerous females, the peak timing of larval release also occurred about 3 days after the new and full moon (3.2 ±

1.3 days) during the intermediate amplitude nocturnal high tide (10.2 ± 6.2 days after the maximum amplitude nocturnal high tides) (Table 1) and lasted for about one week. The timing of larval release seemed to occur around the maximum amplitude diurnal high tides (3.9 ± 6.3 days after the maximum amplitude diurnal high tides), but the r value was 0.56 (Table 1). This suggests that the timing of larval release was less consistent with maximum amplitude diurnal high tides. Relative to the diel rhythm, all females released larvae during the first half of the night and a majority of larval release was between 2000H and 2259H (78%, mean = 21:18 ± 1.2 h, Table 1, Fig. 4A). Relative to the tidal rhythm, all females released larvae during the flood tide and most individuals released larvae within 5 hours before the high slack tide (87%, mean = 4.1 ± 1.4 h, Table 1, Fig. 4B).

E. notatus

Similar to the migration rhythmicity of ovigerous females, the peak timing of larval release also occurred about 20 days after the new moon (20.0 ± 1.3 days) during the intermediate amplitude diurnal/nocturnal high tide (Table 1; Fig. 3B) and lasted for about one week. Relative to the diel rhythm, all females released larvae during the first half of the night and a majority of larval release was between 2000H and 2259H (90%, mean = 20:42 ± 1.0 h, Table 1, Fig. 4C). Relative to the tidal rhythm, all females released larvae during the flood tide and most individuals released larvae within the 6 hours before the high slack tide (99%, mean = -4.6 ± 1.1 h, Table 1, Fig. 4D).

DISCUSSION

Season and duration of breeding migration and larval release

Both *C. carnifex* and *E. notatus* showed seasonal breeding migration and larval release, but the season and duration differed from each other. The main season of breeding migration and larval release of *C. carnifex* occurred over the period between June and September during the rainy season while that of *E. notatus* occurred from September to November at the end of the rainy season and the beginning of the dry season. The breeding season of *C. carnifex* in this study was similar to those of the population in Houwan (Hengchun Peninsula, Taiwan) (Cheng 2012) and most other gecarcinids observed by field surveys of seasonal changes in numbers of crabs, such as *C. guanhumi* (Gifford 1962). *C. hirtipes* (Shokita

Table 1. Timing of seaward migration relative to lunar/semilunar and tidal amplitude as well as timing of larval release relative to lunar, semilunar, tidal amplitude, tidal and light-dark cycle in *Cardisoma carnifex* and *Epigrapsus notatus*

	Seaward migration				Timing of larval release	
	Year 2020		Year 2021			
Environmental cycle	Timing	r	Timing	r	Timing	r
Cardisoma carnifex	(*n* = 1598)		(*n* = 4284)		(*n* = 311)	
Semilunar cycle	○ < 3.3 ± 2.6 day	0.78	○ < 3.2 ± 1.3 day	0.97	○ < 3.2 ± 1.3 day	0.90
Tidal amplitude cycle						
Diurnal	MADT < 1.0 ± 11.0 day	0.42	MADT < 2.8 ± 8.6 day	0.50	MADT < 3.9 ± 6.3 day	0.56
Nocturnal	5.6 ± 6.6 day < MANT	0.50	MANT < 8.9 ± 7.1 day	0.51	MANT < 10.2 ± 6.2 day	0.57
Light-dark cycle	N/A	N/A	N/A	N/A	21:18 ± 1.2	0.95
Tidal cycle	N/A	N/A	N/A	N/A	-4.1 ± 1.4 h < HT	0.93
Epigrapsus notatus	(*n* = 100)		(*n* = 204)		(*n* = 204)	
Lunar cycle	● < 20.5 ± 1.3 day	0.95	● < 20.0 ± 1.3 day	0.97	● < 20.0 ± 1.3 day	0.97
Tidal amplitude cycle						
Diurnal	MADT < 18.6 ± 2.1 day	0.94	MADT < 19.1 ± 1.1 day	0.97	MADT < 19.1 ± 1.1 day	0.97
Nocturnal	MANT < 15.1 ± 1.8 day	0.95	MANT < 15.4 ± 1.5 day	0.95	MANT < 15.4 ± 1.5 day	0.95
Light-dark cycle	N/A	N/A	N/A	N/A	20:42 ± 1.0	0.97
Tidal cycle	N/A	N/A	N/A	N/A	-4.6 ± 1.1 h < HT	0.96

Note: Mean angles were calculated using intervals of one day of lunar, semilunar and tidal amplitude cycles and one hour for tidal cycle, light-dark cycle and sunset time. Angular deviations were represented as ± SD. ●, new moon; ○, full moons; MADT, maximum-amplitude diurnal tides; MANT, maximum-amplitude nocturnal tides; HT, high slack tide. $P < 0.001$ for all Rayleigh's r, except for larval release by *C. carnifex* relative to tidal amplitude cycle ($P < 0.05$). The data used for the analyses were between June and September for *C. carnifex* and between September and October for *E. notatus*. Numbers in the parentheses are the sample sizes.

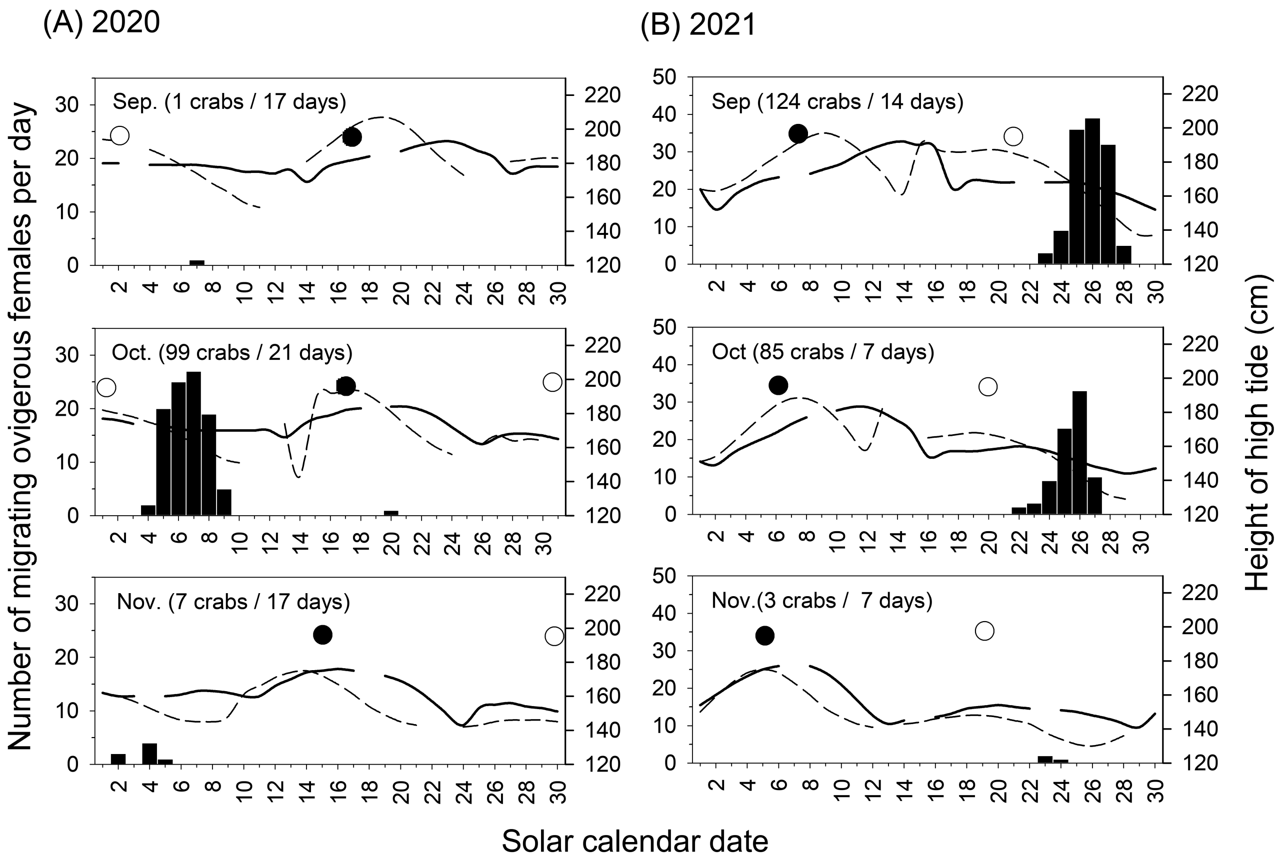

Fig. 3. Temporal pattern of migrating ovigerous female *Epigrapsus notatus* recorded on the embankment flood control road of Chengxi windbreaks between September and November in 2020 (A) and 2021 (B). Solid lines (—) and dash lines (---) represent nocturnal (1800-0559H) and diurnal (0600-1759H) high tides, respectively. The breaks in the lines indicate a lack of data on tidal height for the observation days. Closed and open circles represent new and full moons, respectively.

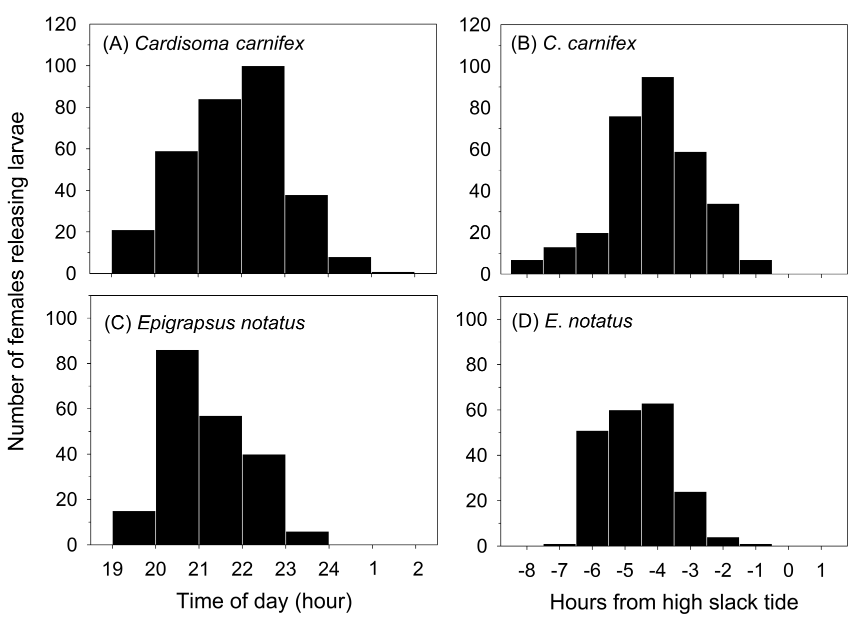

Fig. 4. Temporal change in the number of females releasing larvae between 1800H and 0200H along with the time of the nighttime high tide for *Cardisoma carnifex* (A, B) and *Epigrapsus notatus* (C, D). The total number of female *C. carnifex* and *E. notatus* are 311 and 204, respectively.

1971), *G. natalis* (Hicks 1985), *G. lalandii* (Liu and Jeng 2007) and *J. lagostoma* (Hartnoll et al. 2010). Controlling factors of the breeding season in land crabs may include competition between congeneric species, intertidal zonation, latitude, availability of food and water, rainfall, salinity, temperature, and tidal cycles (Adiyodi 1988; Emmerson 1994). Among these factors, seasonal rainfall appears to be the most important one. Water regulation is crucial for land crabs which cause the timing of migration in most gecarcinids to coincide with the rainy season, possibly to reduce or prevent desiccation stress (Adiyodi 1988).

The season of breeding migration and larval release of *E. notatus* in this study was similar to those of the populations in Gangkou River and Hsiangchiaowan (Hengchun Peninsula, Taiwan), in which ovigerous females migrated to the shore to release larvae from September to November (Wu 2007) or September to October (Liu and Jeng 2005). The late summer-autumn breeding season of *E. notatus* appears to be unusual when compared with other gecarcinids, and the mechanism behind the late breeding activities and relatively shorter duration is not clear. It could be due to the small body size and cryptic lifestyle, such as *E. politus* (Doi et al. 2020). Field observation of the Hsiangchiaowan population shows that these crabs are difficult to find in the coastal forests because they seldom leave their burrows in their residential habitats (Liu and Jeng 2005). The time when they emerge from their burrow is typically during or after rain. At this time, they scavenge leaves and carry them into their burrows. Such a cryptic lifestyle limits the activity of this species and thereby may affect nutrient assimilation during the nonbreeding season, which in turn may lead to late reproduction in this species.

Population rhythms of breeding migration and larval release

Population rhythms of breeding migration and larval release in *Cardisoma carnifex* and *E. notatus* were highly correlated with the lunar/semilunar, light-dark and tidal cycles, but not the tidal amplitude cycle. Regarding the monthly rhythm, *C. carnifex* exhibited a semilunar rhythm following the syzygies and *E. notatus* exhibited a lunar rhythm following the full moon. However, breeding migration and larval release did not occur with the maximum amplitude nocturnal and diurnal high tides in these two species. As for the daily rhythm, they synchronized their breeding migration and larval release to the first half of night and to the flood tides before the high slack tides. This suggests that the lunar cycles and light-dark cycles are the important environmental cues for entraining the breeding rhythms for these two crab species, whereas the tide and tidal amplitude cycles are less important for determining the breeding rhythms.

Lunar/semilunar rhythm

The population rhythms in breeding migration and larval release were semilunar following the syzygies for *C. carnifex* and were lunar following the full moon for *E. notatus*, whereas the spawning activities in these two species did not occur during the periods of maximum amplitude diurnal/nocturnal tides. Both lunar and semilunar rhythms in breeding migration and larval release occur in a wide range of intertidal and supratidal crab species (Forward 1987; Morgan and Christy 1995), but the predominant one for the gecarcinid crabs is the lunar rhythm (Chung 2004; Doi et al. 2020; Hartnoll et al. 2007; Hartnoll et al. 2010; Hicks 1985; Liu and Jeng 2005 2007; Wolcott and Wolcott 1982; Wu 2007). However, there are still some gecarcinid species (or populations) that exhibit a semilunar rhythm like *C. carnifex*, such as *Cardisoma guanhumi* (Gifford 1962) and *Gecarcinus lateralis* (the population on the coast of Colombia) (Klaassen 1975). Compared to other gecarcinids, *C. carnifex* seems to belong to the smaller group that follows the semilunar rhythm.

However, what remains unclear is the relationship between the semilunar rhythm of the female population and the endogenous rhythm of each female in *C. carnifex*. It may be that the semilunar rhythm in the population comes from the endogenous semilunar rhythm of the individual female. Alternatively, the semilunar rhythm in the population could come from the endogenous lunar rhythm of the individual female. In this case, the semilunar rhythm may result from two groups of females: one group that releases larvae during the days around the full moon and another group that is synchronized with the days around the new moon, *i.e.*, a bimodal distribution of larval release. *Sesarma haematocheir* is an example of a species where populations exhibit a semilunar rhythm, but each individual exhibits an endogenous lunar rhythm (Saigusa 1980). In the study, Saigusa maintained female crabs from a population of *S. haematocheir* in the laboratory under a consistent light-dark cycle for several months. The larval release of each female crab was monitored for three consecutive releases and was related to the lunar cycle. The study found that part of the population released the larvae during the full moon while others released during the new moon. Thus, more research is needed to understand the actual breeding rhythm of individual female crabs in *C. carnifex*.

Both fluctuations in tidal amplitude (Christy 1978; Forward 1987; Morgan and Christy 1995 1994) and the lunar cycle (Saigusa 1980 1988; Wolcott and Wolcott 1982) have been suggested to be the proximate cause for the lunar/semilunar reproductive rhythm. Such entrainment to tidal amplitude cycles typically occurs in intertidal crabs whose habitats are regularly inundated by larger amplitude tides (Christy 2011; Morgan and Christy 1995). The most common pattern is that ovigerous females migrate and release larvae at times of the month of maximum amplitude tides (3–1 days before or 1–3 days after the maximum amplitude tide) at night in the biweekly or monthly cycle of tidal amplitude (Bergin 1981; Christy 1982 2011; Morgan 1996b; Morgan and Christy 1995). Alternatively, the semilunar/lunar rhythm of larval release in the supratidal crab (*e.g.*, *Chiromantes haematocheir*) can be entrained by a simulated lunar cycle consisting of a 24 h light-dark cycle and a 24.8 h artificial moonlight cycle in the laboratory regardless of tidal variation (Saigusa 1980 1988). The crab *C. haematocheir* inhabits supralittoral hillsides and paddy fields where it cannot experience the variations of tides directly but would have a clear view of the moon. As far as we know, this species is the only species that the lunar rhythm of reproduction is set by the lunar cycle, independently of the lunar tide amplitude cycle (Saigusa 1980 1988 1992). This is different from most intertidal crabs that use the tidal amplitude cycle as a cue and release the larvae on the maximum or larger amplitude tides in the biweekly or monthly cycle of tidal amplitude (Christy 2011). Morgan and Christy (1995) also suggested that the timing of larval release by supratidal crabs appears to be less coincidently with tidal amplitude cycles than in high intertidal crabs.

In our study, we found that the timing of reproductive rhythms of these two crab species coincided with the syzygies of the moon, but not the maximum amplitude diurnal/nocturnal tides. This implies that the lunar cycle is a more important factor influencing the synchronous breeding migration and larval release than the tidal amplitude for these two crab species. Both *C. carnifex* and *E. notatus* inhabit supratidal habitats (Liu 2020; Liu and Jeng 2005), and they are not directly exposed to tidal fluctuations but would have a clear view of the moon. Thus, as tidally correlated factors appear not to be reliable environmental cues for migration and larval release for terrestrial crab species, responding to the lunar cycles independently of tidal amplitude appears to be a successful adaptation for these two supratidal crab species.

Diel rhythm

Both ovigerous female *C. carnifex* and *E. notatus* migrated to the shore and released larvae in the first half of night during the flood tide a couple of hours before the time of high slack tide. Such nighttime breeding in these two species is similar to most other intertidal and supratidal crabs which also exhibit nocturnal seaward migration and larval release (Christy 2011 1986; Dennenmoser et al. 2020; Forward 1987; Hartnoll et al. 2007; Liu and Jeng 2005). Taking advantage of nighttime may have some adaptive benefits for land crabs. During the night when illumination is poor, the risk of predation on larvae by visual predators may be reduced (Christy 2003; Forward 1987; Morgan 1990). The color and amount of larval pigment may influence the vulnerability of larvae of crabs to planktivorous fishes (Morgan and Christy 1997 1994). Decapods that have larvae with cryptic colors (yellow-green) that make them difficult for fish to see, release their larvae any time day or night, but those with conspicuously colored larvae (red or brownish) release their larvae only at night (Morgan and Christy 1997 1994). Although we have not yet determined the vulnerability of larvae of *C. carnifex* and *E. notatus* to planktivorous fishes, their red to dark red coloration may make them highly visible to foraging fish (Kannupandi et al. 1980) (Chung-Chieh Chang, personal observation), since red contrasts strongly with the background spectral radiance of the green-yellow color in coastal waters (Lythgoe 1979). Thus, the release of larvae during the nighttime in these two species may reduce predation and enhance reproductive success.

Nighttime reproduction may also benefit the adults and larvae by reducing the chance of being exposed to high daytime temperatures (Dollard 1980). Thus, if female crabs release larvae at the beginning of the night, larvae would experience declining temperatures initially, which could be reduced further if larvae were transported by the ebb tides into deeper water. Limiting reproductive activity to the night may also reduce water loss (Wood et al. 1986).

However, the occurrence of breeding migration and larval release during the flood tide in these two species is somewhat different from most other crabs whose activities typically occur near the high tide (Christy 2011; Forward 1987; Liu and Jeng 2005). Most supratidal, tidal and even subtidal crabs choose to release larvae around the time of high tide (Christy 2011; Dennenmoser et al. 2020; Forward 1987). The possible mechanism behind this could be that there is a hierarchy in rhythms of reproductive timing on the basis of the relative degree to which they were entrained by their respective environmental cycles (Morgan 1996a b; Morgan and Christy 1994; Saigusa 1982). Although diel rhythm and tidal rhythm may jointly influence the larval release timing, each rhythm does not exert equal influence (Forward et al. 1986; Morgan and Christy 1997 1994; Saigusa 1981; Saigusa and Hidaka 1978). For example, the timing of larval release of *Cataleptodius floridanus* (Xanthidae) on the Caribbean coast was primarily determined by the light-dark cycle, and they release larvae only at dusk regardless of the phasing of the other environmental cycles. As a result, they release their larvae sometimes during early flood tides or late ebb tides depending on the season (Morgan and Christy 1994). In this study, the light-dark cycle appeared to be a dominant environmental factor determining the larval release timing of *C. carnifex* and *E. notatus* because all of the females released their larvae in the evening, concentrated to the first half of the night. Restricting the release of larvae to the first half of the night following the new and/or full moon precludes the release of larvae during high slack tides because high slack tides occur only after midnight (0000–0600H) during the days of larval release for these two crab species. Thus, both *C. carnifex* and *E. notatus* tracked primarily the light-dark cycle, releasing larvae during the first half of the night, and thereby forsook releasing larvae at or after the high slack tides. This may also suggest that decreased vulnerability to visual predators for larvae by taking advantage of nighttime may be more important than the avoidance of extreme variation in salinity or rapid removal from the shorelines that high tide provides.

CONCLUSIONS

This study revealed the breeding season, dynamics of breeding migration, and timing of larval release of *C. carnifex* and *E. notatus* in the Taijian area. Both species of crabs are seasonal breeders, but the periodicity differs considerably. The breeding season of *C. carnifex* occurred between June and September during the rainy season from September to October while that of *E. notatus* occurred from September to November near the end of the rainy season. The population rhythm in breeding migration and larval release related to the lunar cycle is semilunar during an approximately one-week interval following the syzygy in *C. carnifex* and lunar during an approximately one week interval following the full moon in *E. notatus*. However, the breeding migration and larval release in these two species did not occur with the maximum amplitude nocturnal and diurnal high tides but with the intermediated ones. This suggests that the lunar light cycle is a more important cue than the tidal amplitude cycle. In addition to *C. haematocheir* (Saigusa 1980 1988), our study provides two more crab species that live in the supratidal zone and time their reproduction with respect to the lunar light cycle rather than the amplitudes of the tides. This may be common to many supratidal land crabs but bears further investigation. For the diel rhythm, the breeding migration and larval release of these two crab species therefore prioritized the light-dark cycle over the tidal cycle as a cue (Saigusa 1982). The functional advantage of using nighttime for breeding migration and larval release may be to avoid predators.

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