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Some Reproductive Aspects of *Gecarcoidea lalandii* (Brachyura: Gecarcinidae) in Taiwan

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Hung-Chang Liu and Ming-Shiou Jeng (2007) Some reproductive aspects of *Gecarcoidea lalandii* (Brachyura: Gecarcinidae) in Taiwan. *Zoological Studies* **46**(3): 347-354. The reproductive biology of the land crab *Gecarcoidea lalandii* was documented on the Hengchun Peninsula, southern Taiwan. Ovigerous females have an average carapace width of 57 ± 7 (range, 42-78) mm (*n* = 287). The breeding season is variable, depending on the beginning of the rainy season, and in 2003, it lasted from June to Oct., a relatively longer breeding season than determined for its congener, *G. natalis*. Ovigerous females usually release their larvae during 7-10 d in the last quarter of the lunar cycle. Larval release shows a closer relationship with the timing of sunrise than with the high tide. This species exhibits an unusual larval release behavior while clinging to vertical rock faces in which the ovigerous females drop egg masses into the water without actually entering the water. This unusual larval release from above the water and the choice of surge channels as release sites are thought to be adaptations to life on land which may reduce the risks of mortality to ovigerous females. http://zoolstud.sinica.edu.tw/Journals/46.3/347.pdf

Key words: *Gecarcoidea*, Gecarcinidae, Larval release, Reproduction.

Land crabs have successfully colonized both tropical islands and continental maritime forests, and may have large populations exhibiting high densities (Green 1997, Sherman 2002). Alexander (1979) suggested multiple roles for land crabs in the ecosystems of small islands, including the transfer of energy from land to sea and vice versa, preventing or reducing colonization by exotic plant species, hastening leaf litter breakdown, reducing the number of carrion-breeding flies, aerating the soil, speeding erosion, aiding soil formation, and providing drinking and breeding places for other animals. The abundant land crabs on Christmas I. (Green et al. 1997) and in Costa Rica (Sherman 2002) have been proven to strongly affect seedling diversity in rain forests through their selective seedling consumption. These land crabs are also important in hastening leaf litter breakdown through digestion (O'Dowd and Lake 1989, Sherman 2003). On many small islands, land crabs may even occupy the top of the energy pyramid (Burggren and McMahon 1988).

The robust, heavy-shelled gecarcinid crabs, such as *Cardisoma*, *Gecarcinus*, and *Gecarcoidea*, are often the subjects when the term "land crab" is used without elaboration (Hartnoll 1988). These crabs are medium- to large-sized individuals, with large *Gecarcoidea natalis* (Pocock) reaching 120 mm in carapace width (Green 1997). The Gecarcinidae currently consists of 20 species and has been recognized to include 4 (Hartnoll 1988) or 6 genera (Ng and Guinot 2001). Although all species of the Gecarcinidae show distinct terrestrial adaptations, their eggs have to hatch in the sea, where the larvae undergo typical planktonic development (Hartnoll 1988). The mass migration of reproductive individuals to the surf for larval release has been reported for many gecarcinid species, such as *Cardisoma guanhumi* (Latreille) (Henning 1975), *Cardisoma hirtipes* Dana (Shokita

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1971), *Gecarcinus lateralis* (Freminville) (Bliss et al. 1978, Wolcott and Wolcott 1982), and *Gecarcoidea natalis* (Hicks 1985, Adamczewska and Morris 2001). Such breeding migrations to the sea are highly synchronized with lunar and seasonal cycles (Johnson 1965, Shokita 1971, Hicks 1985). Reproductive synchrony is a common phenomenon among coastal land crabs and is believed to be under the control of environmental cycles that occur with predictable regularity. The most important factors that influence marine animals are the light-dark cycle, tidal cycle, tidal amplitude cycle, and lunar cycle (Morgan and Christy 1995). Most crabs living close to the high tidal zone prefer to release larvae during the largest-amplitude nocturnal high-tide period (Morgan 1995). Planktivorous fish are believed to be the most important selective agents influencing the reproductive synchrony of these crabs (Morgan and Christy 1994 1997).

Gecarcoidea consists only of 2 species and is confined to the Indo-Pacific region. The distribution of *G. natalis* is limited to Christmas I. and Cocos I. in the Indian Ocean (Hicks et al. 1990). *Gecarcoidea lalandii* H. Milne Edwards has a wider distribution in the Indo-West Pacific islands starting from the Andaman Is. eastward (Hartnoll 1988). Previous studies on *G. natalis* are numerous including physiological research (Adamczewska and Morris 1994, Adamczewskad and Morris 1998), and breeding migration and behavioral studies (Hicks 1985, O'Dowd and Lake 1989, Green 1997, Adamczewska and Morris 2001). In contrast, very few ecological studies on *G. lalandii* have been conducted, although it has a wider distribution, and abundant populations have been described on Jarak I. (Audy et al. 1950), Pulau Aor, and Pulau Ular in Malaysia (Johnson 1965). The aim of this study was to describe the reproductive biology of *G. lalandii*, including population data, breeding season, and larval release timing and behavior, with particular focus on the unusual larval release behavior carried out from above the water surface that is unique to *Gecarcoidea*. We also propose an explanation for the timing and behavior of larval release of *G. lalandii*.

MATERIALS AND METHODS

The study was conducted at Hsiangchiaowan, (21°55'30"N, 120°49'31"E), Hengchun Peninsula, Pingtung County, southern Taiwan. There is a coastal forest about 2 km long in this area. Twenty species of land crabs have been recorded within the forest, including 2 recently reported arboreal species. Nine of them have sufficiently large populations which are suitable for reproductive biological research such as that carried out by the authors since 1995.

To study the timing and behavior of larval release, a 100 x 30 m rectangular portion of the supralittoral and littoral zones outside the coastal forest was marked and regularly monitored. This area has a gently sloping profile of rugged, fossil coral reefs with many crevices and rock pools. The site is interspersed with 8 roughly parallel surge channels, two of which touch the edge of the forest, while the others reach about halfway up into the supralittoral zone. These surge channels are marked by precipitous cliffs of up to 3 m high.

A thorough, month-long continuous observation, carried out from Sept. 1 to Oct. 4, 2002, established that larval release in *G. lalandii* occurs during the last quarter of the lunar cycle. Larval release of *G. lalandii* during the last quarter of the lunar cycle in May 2003 was monitored, but no ovigerous females of *G. lalandii* were observed because of a delay in the rainy season. Observations were conducted during the 2 wk following each full moon from June to Dec. 2003.

The timing of larval release and the behavior of ovigerous females were observed and recorded. After ovigerous females had released their larvae, the females were caught, measured, marked on the carapace, and released. The following information was taken and recorded for each crab encountered: sex, carapace width (CW), carapace length, maximum height of the propodite of each cheliped, abdominal width (between the 4th and 5th abdominal segments), and body weight. Not all crabs were suitable for measurement because of the loss of various appendages. Size at maturity for females was determined both from the morphology of the abdomen and from the smallest size of ovigerous females. After being measured, the crabs were marked on the carapace with different colored marking pens in different months, and released back into their original habitats.

Fecundity data were taken from 23 migrating ovigerous females, who were captured at the surf zone before midnight and brought back to the laboratory. The weight of each ovigerous female was determined. After larval release in the laboratory, the weight of the females was measured again. The number of eggs in 0.05 g eggs of the egg mass was counted for 5 ovigerous females, and the total number of released larvae from each female was calculated.

In order to understand the relationship between the reproduction of *G. lalandii* and the local climate, seasonal precipitation data were obtained from a weather station at Kenting (located at 21°56'52"N, 120°47'39"E), about 4 km from the study area, while seasonal temperature data were obtained from a weather station at Hengchun (located at 22°00'20"N, 120°44'17"E), about 13 km from the study area. Tidal data were obtained from a meteorological station at Houpihu (located at 21°56'50"N, 120°44'14"E), about 9 km away.

RESULTS

Population information

Gecarcoidea lalandii lives within the forest and can be found in open fields after a rain or during the breeding season. Within the forest, both male and female crabs are active outside the burrows at night but never in large numbers at the same time. Juveniles were seldom found in the forest even under rocks. Ovigerous females with eggs showing early development were never found to be active in the forest; they presumably hide deeper underground and never emerge. In contrast, females that are ready to release larvae can easily be found in the littoral zone.

Ovigerous females have an average CW of 57 ± 7 mm (mean ± standard deviation), range 42-78 mm (n = 287) (Fig. 1). It was found that the morphology of the abdomen was not a reliable character to determine the maturity of females. There was no significant difference among CW-body weight correlation values taken in the different sampled months suggesting that ovigerous females feed even during the spawning period.

Migration of ovigerous females

Ovigerous females were only found to migrate to the shore at night, and most of them appeared in the surf zone a few minutes before actual larval release. During the migration, ovigerous females avoided all standing water of any salinity, thereby preventing accidental larval release in diluted or concentrated tidepools. These females also never showed any dipping behavior in the seawater or tidepools before or after actual larval release. No weak or dead females as a result of desiccation were encountered along their migration route during the study period. During migration, females were sensitive to light and would take temporary refuge in crevices if illuminated. Even when the larvae were ready for hatching, the ovigerous females would still hide in crevices when subjected to continued light disturbance. Bad weather and heavy rain did not affect the migration of ovigerous females.

After females had reached the surf zone, they waited 1-2 m from the water until the larvae were ready for hatching. The waiting time lasted from a few minutes to a few hours. Some females even remained at the surf zone until the following night to release their larvae. Some males could be seen in the surf zone together with ovigerous females, but no mating or courtship behavior was ever observed after females released their larvae. After larval release, the females immediately returned and entered the coastal forest.

Body size is important for the safety of ovigerous females in their migration to the surf zone. Smaller ovigerous females might encounter greater risks from predators, but larger females were never found to have been victimized. One small ovigerous female (CW 43.5 mm) was attacked by *Geograpsus crinipes* (Dana) (CW 55.6 mm). Remnants of 2 other females were also found in the surf zone, most likely attacked by *Geograpsus crinipes* as well.

Breeding season

The breeding season of *G. lalandii* was from June to Oct. in 2003. The total number of oviger-

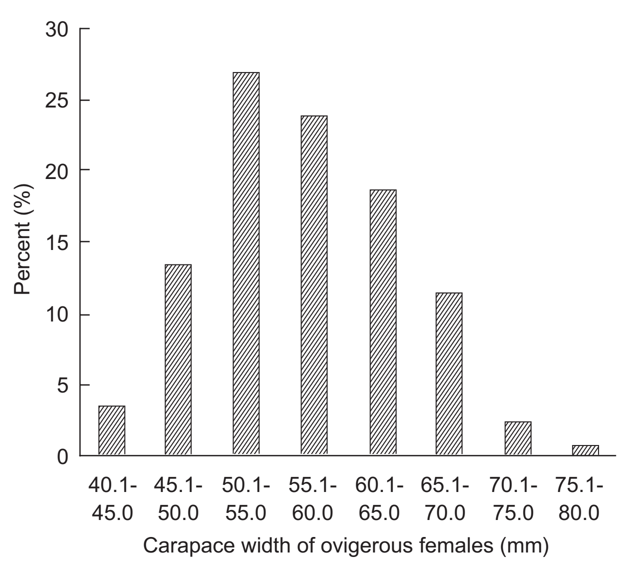

Fig. 1. Population size-frequency distributions (%) of breeding females of *Gecarcoidea lalandii* (n = 287).

ous females observed was 438 (Fig. 2), with the highest number in July (n = 188). Only 2 ovigerous females were found in Oct. In other years, migrating ovigerous females were found beginning in mid-May (1998) and disappearing in early Sept. (2002). The breeding season here roughly represents the period when female crabs are found to release their larvae into the water. Because almost no ovigerous females in the early stages were found in the field, it is difficult to determine the incubation period of eggs in the breeding season.

The breeding season of *G. lalandii* begins with the onset of the rainy season and ends approximately with the end of the rainy season. In the study area, the average annual temperature exceeds 20°C; thus land crabs can be found to be active after a rain even during the winter. The rainy season usually begins in May or June. Typhoons bring heavy rains almost every summer. In 1998, the rainy season began in May and ovigerous females of *G. lalandii* were observed to go to the surf zone for larval release at that time. In 2003, the rainy season did not begin until June, and females releasing larvae also appeared at that time. This reveals that *G. lalandii* becomes reproductively ready before the end of the dry season. Rain is rare after Sept. in the study area unless a typhoon occurs. In 2002, the rainy season ended in Sept., and the reproductive activities of ovigerous females of *G. lalandii* had ceased by early Sept. In 2003, reproduction activities had ended by Oct. coinciding with the end of the rainy season that year. No female releasing larvae was observed following the abundant rain in Nov. 2003 associated with a typhoon.

Timing of larval release

Ovigerous females of *G. lalandii* follow a lunar rhythm, releasing larvae during the last quarter of the lunar month (Fig. 2). Larval release usually lasts for 7-10 d within a lunar cycle with peaks occurring 3-5 d before a new moon.

Larval release coincided more with the timing of sunrise than with the maximum tides which consistently occurred 1-2 h before sunrise (Fig. 3). Most ovigerous females appeared in the surf zone after midnight where they waited a few minutes before releasing their larvae. Some females (~15%) reached the surf zone before midnight and waited a few hours before releasing their larvae. A few females remained in the surf zone until the following night before they released their larvae.

Larval release behavior

Gecarcoidea lalandii shows 2 different types of larval release. The 1st type of behavior takes place in the water similar to the usual behavior exhibited by most Brachyura. When the eggs are ready for hatching, ovigerous females of *G. lalandii* walk into shallow water, by climbing down on cliffs or standing on the sea bottom. The release process involves a rapid fanning movement of the abdomen which lasts for a few seconds. In many

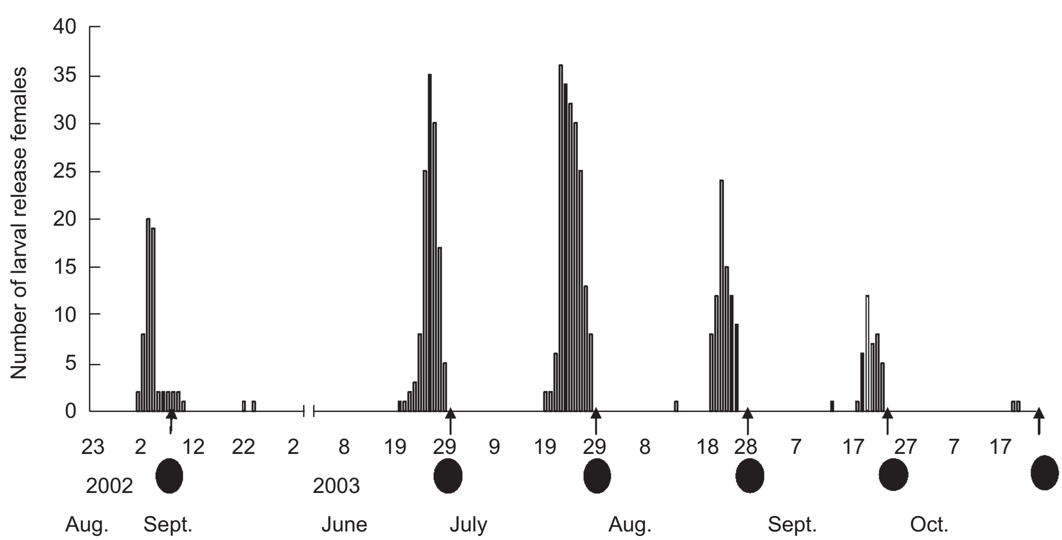

Fig. 2. Daily larval release patterns of *Gecarcoidea lalandii* in Sept. 2002 and June-Oct. 2003. Closed circles represent new moon phases. (n = 500).

cases, ovigerous females do not directly enter the water. They stay just a few centimeters above the water level, where they wait for incoming waves. These females usually submerge the lower half of the body and rapidly move their abdomen back and forth during the brief period of submergence. These females sometimes have a dry carapace even after larval release.

The 2nd type of larval release takes place outside the water (Fig. 4). During the larval release period, females stand on the cliff above the water, grasping the cliff surface with only their walking legs. Facing down towards the water surface with claws outstretched, the entire body is oriented at a right angle to the rock surface and the fanning movement of the abdomen proceeds slowly. After a few seconds, the entire egg mass suddenly drops into the water. With the floating egg masses on the water surface, the larvae leave the egg masses one by one until finally, only empty egg cases and some unhatched eggs are left on the water surface. The entire process lasts a few seconds to a few minutes. In many cases, ovigerous females drop their egg masses on land just above the water, particularly when disturbed.

In both types of larval release behavior, after larval release, the abdominal pouch of the females contained no remnants of unhatched eggs or empty egg cases attached to their appendages.

Gecarcoidea lalandii prefers to release larvae in surge channels rather than along the exposed shore in the study area. Most females release larvae within the landward and middle portions of the surge channels, with very few releases observed in the exposed surf zone.

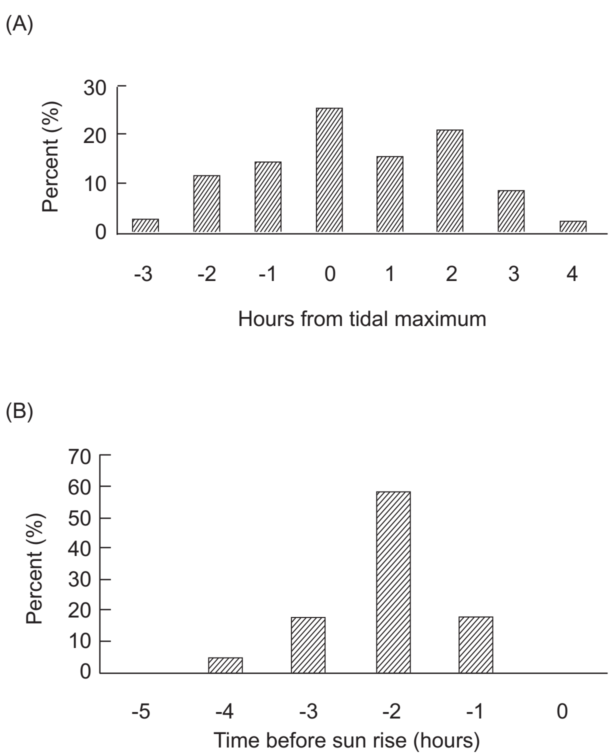

Fig. 3. (A) Number of females of *Gecarcoidea lalandii* releasing larvae versus the time of the evening high tide: 0 corresponds to high tide; -1 and 1 mean 1 h before and after high tide time, etc. (B) Number of females of *G. lalandii* releasing larvae versus the time of sunrise: 0 means larvae were released at the same hour as sunrise; -1 means 1 h before sunrise, etc.

Fecundity

The number of developed larvae carried by females varies between 70,000 and 210,000 depending on the size of the female, with fecundity directly increasing with size up to 65 mm CW, then falling slightly (Fig. 5).

Some females can reproduce at least twice within a single reproduction season. As all captured ovigerous females were marked with different colors and numbers corresponding to different months, it was easy to detect females that had released larvae more than once during a reproductive season. For instance, 2 females marked in June were recaptured in July. Another 3 marked females caught in July were recaptured in Sept. However, the marks on the carapaces of females did not remain through the entire breeding season. Thus, no precise data on the proportion of females which reproduced more than once can be provided.

Fig. 4. A female *Gecarcoidea lalandii* releasing its larvae from above the water surface.

DISCUSSION

Both species of *Gecarcoidea* have unusual larval release behaviors from above the water which have never been reported in any other Brachyura. Ovigerous females of *G. natalis* were observed to stand above the water and drop eggs into the water from cliffs (1-8 m) above the water (Hicks 1985). The release of larvae from above the water can be thought of as an adaptation to life on land in *Gecarcoidea*, which can reduce the chances of ovigerous females being swept away by the waves. Ovigerous females of *Epigrapsus* have also developed an unusual larval release behavior. They shake the entire body to release larvae instead of utilizing the fanning motion of the abdomen. According to a preliminary study on the larval release behavior of *G. lalandii* and *Epigrapsus*, we hypothesized that this behavior serves to lower the mortality risks for ovigerous females of gecarcinid crabs. Both *E. notatus* and *G. lalandii* prefer to release their larvae inside surge channels where the effects of wave action are less threatening compared with the exposed surf zone, thereby providing a safer environment for the females. However, the presence of newly released larvae inside surge channels attracts many predatory fish. Thus, larval release in surge channels can bring protective benefits for the mothers but raise mortality risks for the larvae. The higher mortality of larvae can perhaps be offset by multiple, more-prolonged reproductive seasons and longer life exhibited by these crabs.

Most crabs release larvae during or shortly after the high slack tide, and therefore zonation does not influence the timing of larval release relative to the tidal cycle (Morgan 1995). Predation by visual predators may best explain the hatching patterns of crabs with ovigerous females, embryos, and larvae all risking predation during larval release (Morgan and Christy 1994 1995 1997). Larval release after the high tide period has been reported in some gecarcinids. In *Epigrapsus notatus* in Taiwan, release of larvae was observed during high tide and continued for about 2 h (Liu and Jeng 2005). The peak of larval release of *C. hirtipes* in Okinawa also occurs about 1 h after the highest tide (Shokita 1971). The time of significant larval release of *G. natalis* takes place in the early morning around 20 min before high tide and lasts for 3 h with peak activity observed at the time when the tide has begun to recede (Hicks 1985). But, in *Gecarcinus lateralis*, the majority of ovigerous females appear on the shore between 21:00 and 24:00 on the 4th or 5th night following a full moon, regardless of tidal conditions (Wolcott and Wolcott 1982). In *G. lalandii*, the timing of larval release shows a close relationship with sunrise rather than the highest tide.

The most obvious behavioral difference between *G. natalis* and *G. lalandii* is that the former is active during daylight hours (Green 1997), while *G. lalandii* is mainly nocturnal even on small remote islands (Audy et al. 1950). There are further differences in their reproductive biology. First of all, the breeding season of *G. lalandii* is longer compared to that of *G. natalis*. Although both species have reproductive cycles that begin at the onset of the rainy season, the breeding season of *G. lalandii* lasts longer and ends almost at the same time as the rainy season tapers off. Second, the shoreward migration of ovigerous females of *G. natalis* peaks in the morning and late afternoon, with little activity at night or midday, and they release their larvae about 18 h after leaving the burrow (Hicks 1985). However, *G. lalandii* only moves at night and most of them only spend a few minutes in the surf zone. Ovigerous females of *G. lalandii* are sensitive to light and take temporary refuge in crevices if illuminated, but ovigerous females of *G. natalis* are attracted to light (unpubl. data). Large numbers of *G. natalis* have been observed engaged in immersion behavior in the ocean during the process of reproductive migration (Hicks 1985), but such immersion behavior has never been observed in *G. lalandii* until now. Actually, *G. lalandii* prefers fresh water under both normal and hemo-concentrated body conditions in lab experiments (Combs et al. 1992). *Gecarcoidea*

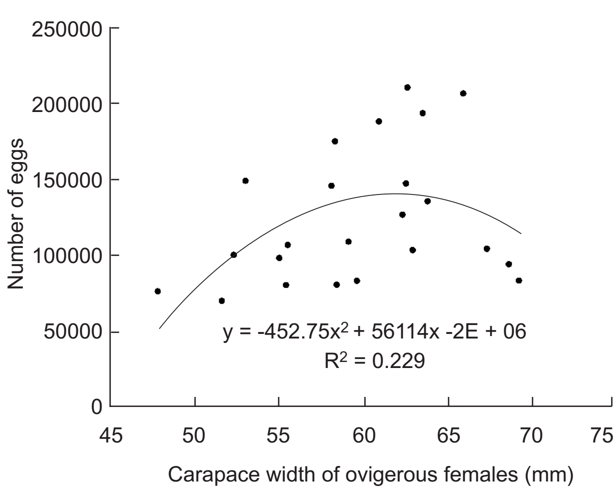

Fig. 5. The relationship between egg number and carapace width in *Gecarcoidea lalandii* females.

natalis migrates en masse to the lower terraces before mating and larval release (Hicks 1985), but no such migration has been observed in *G. lalandii* in Taiwan. The last point that both Hicks (1985) and Green (1997) suggested was perhaps that only half of *G. natalis* adults participate in the reproductive migratory process as evidenced by a comparison of pre- and post-migration activity data in the plateau forest. In contrast, at least some *G. lalandii* females can reproduce twice within a reproductive season. It is likely that these 2 species exhibit different survival strategies. *Gecarcoidea lalandii* expends more energy on reproduction, while *G. natalis* spends more energy on growth, such that a majority of the crabs exhibit molting at the end of the wet season (Hicks et al. 1990) and can grow to 12 cm in CW (Green 1997).

Two major groups can be distinguished within the Gecarcinidae according to larval morphology: the first group consists of *Epigrapsus*, *Gecarcinus*, and *Gecarcoidea*, and the second group is comprised of the genus *Cardisoma* (Cuesta et al. 2002). The length of the breeding season also shows the same divergent tendency. Species of *Cardisoma* usually have a longer breeding season compared to other gecarcinids. *Cardisoma guanhumi* in south Florida breeds from June or early July to Dec., with peaks in Sept. and Oct. (Gifford 1962). *Cardisoma hirtipes* in Okinawa migrates to the sea to release larvae from June to Nov. (Shokita and Shikatani 1990), and the breeding activity of *C. carnifex* (Herbst) on Aldabra I. also lasts for 6 lunar cycles (Grubb 1971). On the other hand, the breeding season of *Epigrapsus notatus* (Heller) only lasts for 2 mo (Liu and Jeng 2005). The breeding season of *Epigrapsus politus* Heller is likewise short from Aug. to Oct., with very few females reproducing in Aug. (unpubl. data). The breeding activity of *G. natalis* also lasts for 2 or 3 lunar cycles with only 1 marked by major reproductive activity (Hicks 1985). *Gecarcoidea lalandii* has a longer breeding season which lasts 4-5 mo. The burrows of *G. lateralis* do not extend down to groundwater level (Bliss and Mantel 1968), and the same can be said for both *Epigrapsus* (Liu and Jeng 2005) and *Gecarcoidea*. However, the burrows of *C. guanhumi* extend down to the groundwater and serve as water supply depots where the crab can obtain water without being limited to surface deposits (Herreid and Gifford 1963). This is probably one reason why *Cardisoma* has a longer breeding season compared to other gecarcinids.

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