Seaward migration and larval release of the land hermit crab
Coenobita brevimanus Dana, 1852 (Anomura: Coenobitidae)
on Iriomote Island, Japan

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Abstract.— The seaward migration and larval release of Coenobita brevimanus Dana, 1852 on a sandy beach of Iriomote Island, Japan, was studied between May and November 2009 and between May and December 2010. Seaward migration and larval release were mainly observed for several days before and after new moons during the period from June to November, and the migration was mainly focused on 0.82 days after the new moon. Around full moons, some crabs were also found, with the highest numbers at 1.34 days after spring tides (semi-lunar rhythms). Almost half of the crabs that appeared on the beach entered seawater, and almost half of the immersed crabs released zoeas or exhibited swinging behavior. Appearance of crabs on the beach and entering seawater occurred only after sunset between 19:00 to 23:10. The peak time of the appearance on the beach was within a certain range each month. Crabs entered seawater at a mean of 2 h after the nighttime high tide. Seaward migration of the crabs showed clear seasonality, and many crabs migrated and entered seawater during the period from July to September, the months with higher temperature (≥25°C). This species shows a phenology and rhythm of spawning common to coenobitids on the Ryukyu Islands.

Key words: hatch, reproduction, Ryukyu Islands, spawning, Yaeyama Islands

Introduction

As a taxon, the family Coenobitidae inhabits the largest terrestrial area of the anomuran decapods and has worldwide subtropical and tropical distribution. They are found on shores, inland areas, coastal forests, rainforests and arid scrublands of small islands or narrow coastal strips (Hartnoll, 1988; Greenaway, 2003). Because their aquatic larvae need saline water to hatch (Hamasaki et al., 2018a), ovigerous females of coenobitids move to the water’s edge and release larvae into seawater (Yamaguchi, 1938; de Wilde, 1973; Imafuku, 2001; Nakasone, 2001; Nieves-Rivera & Williams, 2003; Doi et al., 2016, 2018a). Larval release by coenobitid crabs takes place in the swash zone, which allows us to directly observe those behaviors, unlike aquatic species, which release larvae underwater. In addition, ovigerous females of coenobitids migrate at a slower walking speed on beaches with poor vegetation cover. Therefore, members of this family are easier to observe than intertidal and supratidal brachyurans which can move more quickly.

The general biology and chronobiology of spawning have been well documented in field studies of brachyurans (e.g., Forward, 1987; Morgan, 1995; Christy, 2011). In the case of littoral and supralittoral brachyurans, larval release generally occurs at night during high tide on larger amplitude tides on a bi-weekly or monthly cycle of the tidal amplitude (Christy,
The larval release by coenobitids has been documented with respect to the lunar cycle but not the tidal amplitude cycle (de Wilde, 1973; Nakasone, 2001; Nieve-Rivera & Williams, 2003; Sato & Yoseda, 2009; Doi et al., 2016). Spatiotemporal patterns of larval release are important parameters that determine the survival and transport of early-stage larvae by currents (Christy, 2003, Murakami et al., 2014; Doi et al., 2018). Moreover, expansion of the geographical distribution and metapopulation network of benthic populations of terrestrial decapods including coenobitids is determined by the transport of aquatic larvae (Anger, 2006). Therefore, characterizing the dynamics of larval release by coenobitids is indispensable for understanding the population structure.

The land hermit crab *Coenobita brevimanus* Dana, 1852 (Anomura: Coenobitidae) is widely distributed and a common species throughout the Indo-Pacific area (Hartnoll, 1988; Vannini & Ferretti, 1997; McLaughlin et al., 2007; Hamasaki et al., 2015a; Hsu et al., 2018). The southern islands of the Japanese archipelago are the extreme northern limit of the biological range of this species. In the Ryukyu Islands, *C. brevimanus* is scarce in the northern part, but some local populations of this species are found in the southern part, the Yaeyama Islands (Okinawa Prefectural Board of Education, 1987; 2006). In this area, *C. brevimanus* is the most terrestrially adapted *Coenobita* and inhabits inland and coastal forests in lower density than its sympatric congener *C. cavipes* (Kosuge & Kohno, 2010; Hamasaki et al., 2017). The abundance of *C. brevimanus* is higher in the area with human settlement (maintained and abandoned villages) and the adjacent beach (Kosuge & Kohno, 2010; Mizutani et al., 2012) than in natural habitats such as on sandy beaches and mangrove estuaries (Kohn et al., 2012; Fujikawa et al., 2017).

The population of *C. brevimanus* in Amitori Bay of Iriomote Island in the Yaeyama Islands (24°24′N, 123°46′E) (Fig. 1) has many crabs of large size (Mizutani & Kohno, 2012; Doi et al., 2019). It could serve as a population source to other areas in the northern marginal part of the range through dispersal during pelagic larval stages, because larger females can be expected to have higher fecundity and, thus, release...
more larvae. To consider conservation of the near-threatened *C. brevimanus* in this area (Ministry of the Environment, Japan, 2019) with fragmented distribution, it is necessary to elucidate the dynamics of recruitment and the transition from sea to land of juveniles through pelagic larval stages.

The aim of this investigation was to analyze the temporal changes in seaward migration and spawning in an effort to understand the reproductive biology of *C. brevimanus* and to determine the role of the local Amitori population as a source of the larvae. Field surveys were conducted at different times under different tidal conditions on a sandy beach of Iriomote Island.

**Materials and Methods**

**Study site**

The study area, Amitori Bay, an inlet measuring 2.3 km wide and 3.5 km long, is on the northwestern coast of Iriomote Island (24°24’ N, 123°46’E) in the Yeayama Islands (Fig. 1). On the western coast of this bay, Amitori Village, which was inhabited by a maximum of 200 people between the 17th century and 1971, is situated. In the areas around this village, many large-sized *C. brevimanus* greater than 20 mm in palm width that that were utilize the shells of edible gastropods such as the silver-mouthed turban *Turbo argyrostomus* that were discarded by former residents (Doi *et al.*, 2019). Some individuals of *C. brevimanus* have been documented to migrate to the beach in front of the village and release larvae, but descriptions of the larval release are brief and cover limited periods of observation (Mizutani & Kohno, 2012; Murakami *et al.*, 2014; Nio *et al.*, 2014).

Sampling was conducted on an area of sandy beach near Amitori (hereinafter referred to as Amitori Beach) with a length of 300 m (Fig. 1B). The monthly mean air temperature at Amitori ranged from 18.2 to 28.8°C in 2009 and 18.9 to 29.1°C in 2010, recorded at 10-min intervals using Thermochron SL (KN Laboratories, Inc.) (Fig. 2). Monthly precipitation on Iriomote Island ranged from 71 to 419 mm in 2009 and 40 to 500 mm in 2010 (Fig. 3), as recorded on a meteorological station (24°25.6’N, 123°45.9’E) on Iriomote Island during 2009 (black bars) and 2010 (gray bars). Data were obtained from the Japan Meteorological Agency website (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php).
123°45.9'E) on Iriomote Island and available on the Japan Meteorological Agency (JMA) website (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php). Astronomical tide level data for the study site was obtained from the JMA website (http://www.data.jma.go.jp/kaiyou/db/tide/suisan/).

Field observations
From May to November 2009, a single researcher walked and searched for crabs along a 300 m long stretch of shoreline with sandy beach in Amitori (Fig. 1B) every 2 h from sunset to 6 am on a couple of days before and after the new moon and full moon and during other lunar periods (95 days in total). The times and locations where crabs were found were recorded, and the anterior and whole parts of crabs were photographed in order to identify individuals to the species level.

From May to December 2010, two researchers conducted field surveys to observe crabs migrating on a 180-m long stretch of the beach (Fig. 1B). They patrolled on the artificial revetment neighboring the beach from sunset until 0:00 for a couple of days before and after the new moon and full moon and during other lunar periods (98 days in total). These survey hours were selected because most crabs migrated to the beach near the revetment between sunset and midnight in the 2009 survey. Some behavioral patterns by individual crabs on the beach were occasionally observed on the beach. Before crabs walked back to dune plants, the anterior and whole parts of crabs were photographed for species identification. The times at which crabs appeared on the beach and entered the sea were recorded on selected days in new moon periods. The weather conditions during the observations in the 2010 survey were relatively constant. The air temperature ranged from 25.7 to 33.0°C (Fig. S1), and wind velocity ranged from 0.6–7.1 m/s (Fig. S2). It rained a little (<1.0 mm/h) for 2 and 3 h on only two days (8 and 9 September).

Statistical analysis
To determine whether intervals of seaward-migration/larval release for C. brevimanus are correlated with lunar (29.5 days) or semi-lunar (14.8 days) cycles or with the size of the spring tides, circular plots of the timing of reproduction with phases of the moon and with the spring-neap tidal cycles (14.8-day cycles of the difference in height between high and low tides taken over a day) were used (Collin et al. 2017). The number of crawling/releasing crabs encountered on each date was plotted against dates (degrees) with the new moon or the spring tides as 0°. Circular summary statistics (mean and resultant length) were calculated, and uniformity was tested against the null hypothesis that the larva-releasing circular data were distributed in a uniform pattern with unknown or a specified mean direction by Rayleigh’s test using the circular package (Agostinelli & Lund, 2017) in R, version 3.4.1 (R core team, 2018).

Results
Seasonal changes in number of migrating crabs
A total of 1546 C. brevimanus were observed migrating to the sandy beach during the 2 years of research. The migration occurred between 10 May and 21 October in 2009 (n = 639) and between 13 May and 7 November in 2010 (n = 907) (Fig. 4). The beginning of the main migration season was July, but the season ended in September in 2009 and October in 2010. Only one individual was found during the 5 survey days in November 2010. There were no migrating crabs on the 7 and 4 survey days in November 2009 and December 2010, respectively. The monthly number of seaward migrating crabs increased drastically from July, peaked in August and/or September, and then decreased abruptly in October or November. The tidal amplitude range (tidal level at nighttime high tide to succeeding low tide) was
greater in the new moon period than in the full moon period for both years (Fig. 5).

**Synchronization of seaward migration**

The daily number of seaward migrating crabs varied with the tidal phase and lunar age (Fig. 6). In the spring tide around the new moon phase, 0 to 68 crabs were found in 2009 \((n = 39\) days), and 0 to 84 crabs were found in 2010 \((n = 47\) days). In the spring tide around the full moon phase, 0 to 18 crabs were found in 2009 \((n = 35\) days), and 0 to 10 crabs were found in 2010 \((n = 36\) days). In the neap tides, 0 to 19 crabs were found in 2009 \((n = 48\) days), and 0 to 7 crabs were found in 2010 \((n = 13\) days).

Differences in seaward migration across the lunar and the semi-lunar cycles significantly differed from a uniform distribution for both...
From the values of mean degree, the migration occurred 0.82 days after the new moon and 1.34 days after the spring tide. Concentrations of seaward migration (mean resultant length) were similar for both the lunar cycle and the semi-lunar cycle.

**Behavior on sandy beach**

In 2010, the behavior of crabs on the beach was divided into four patterns: (1) Larvae releasing: crabs walked towards the sea and stopped when incoming waves reached them or they were fully immersed in seawater (< 50 cm depth). When waves washed and submerged the crabs, their bodies swung back and forth. Emerging zoeae from the shell aperture were observed by naked eye ($n = 134$). (2) Immersing and swinging: immersed crabs were swinging back and forth, but zoeas were not confirmed by naked eye observation ($n = 66$). (3) Immersing: crabs immersed themselves fully in seawater, but larvae and swinging were not confirmed by naked eye observation ($n = 208$). (4) Crawling: crabs crawled on the beach and returned to vegetation farther back on the beach without entering seawater ($n = 499$).

**Timing of females appearing on the beach and entering seawater**

Appearance on the beach and entering seawater occurred only after sunset, and the time range was 19:00–23:10 h (Fig. 8). The peak time of appearance on the beach was within a certain range each month, except for in September, and it was not necessarily synchronized to the nighttime high tide. The range of peak appearance time was 20:00–20:30 h in July, 20:30–21:00 in August, and 19:00–21:30 h in October. In September, of the 5 days on which seaward migration was observed, the
peak time was not clearly observed on the first two days. The peak time was 21:30–22:00 on 8 September, and on the following 2 days, it was shifted earlier to 19:20 h. A single peak or several consecutive peaks were observed most days. The mean time showed a similar trend as peak time, and the values were within a certain range each month, with later times in August and earlier times in October (Table 2A). Except for the day when a few crabs appeared (5 October), the timing of the appearance was significantly focused to a specific time and the mean resultant length had a high value (>0.94).

Many crabs entered seawater after the nighttime high tide (Fig. 8), and some days showed no clear peak in the time of entering into the sea. The mean time shifted slightly (10–20 min/day) from earlier to later on most days, except for July (Table 2B). The mean time of immersion was within 2 h after high tide. Except for the day a few crabs appeared (6 September), the time of immersion was significantly focused to a specific time, and the mean resultant length was high (>0.96).

**Discussion**

Seaward migration of *C. brevimanus* showed clear seasonality, and many crabs migrated and entered into seawater in July to September.
when seawater temperature and monthly precipitation were higher (>25°C and >200 or 100 mm), but only a few crabs were found on the beach in months with lower temperature and precipitation (May, June and November). This pattern was similar to the seasonal changes in the number of crabs observed by field survey on Ishigaki Island (Kosuge & Kohno, 2010) and Taiwan (Hsu et al., 2018). The peak period of seaward migration between July and September is the reproductive season for other coenobitid crabs on Yeayama Islands (Sato & Yoseda, 2008, 2013; Doi et al., 2016, 2018a). Seaward migration was not observed when the air temperature was lower than 15°C, which is the temperature at which *C. brevimanus* ceases to be active (McMahon & Burggren, 1981).

Nocturnal coenobitid crabs migrate to the shore for reproduction, ingesting water, and foraging during the night (Harnoll, 1988;
Greenaway, 2003). Almost half of *C. brevimanus* that entered into seawater were confirmed to release zoeas or to exhibit swinging behavior for spawning. In the same season, larval release of *C. brevimanus* was observed at the study site (Mizutani & Kohno, 2012; Nio et al., 2014). The purpose of the seaward migration and entering into seawater for most of the immersed crabs was probably for releasing larvae.

Based on the temperature during the main reproductive season (Fig. 2), the incubation period of *C. brevimanus* is estimated to be about 1 month (Hamasaki et al., 2016). Therefore, the annual number of spawnings per individual is theoretically at most three, but this should be confirmed by mark-recapture experiments. Populations of *Coenobita* that live inland migrate to coastal breeding sites where mating is believed to take place (Greenaway, 2003). Sato & Yoseda (2013) observed that male *B. latro* migrated to coastal breeding sites for future mating opportunities within the reproductive season. Therefore, the crabs showing crawling but not immersion may be males that migrated for mating with post-spawning females.

Tsuru et al. (2018) described diel migration of *C. brevimanus* between inland and coastal forests during the daytime and the seashore at nighttime, and they assumed that the reasons for the migration were reproduction and drinking seawater because juveniles were also found on the seashore. However, the osmotic concentration of serum of *C. brevimanus* was an average of 80.3%, demonstrating that *C. brevimanus* does not depend on the sea for a source of water (Gross, 1964). Unlike beach dwelling coenobitids, *C. brevimanus* can distinguish the odor of fresh water from that of seawater, and they intake only freshwater (Vannini & Ferretti, 1997; Greenaway, 2003). Inland-dwelling *C.

| Date       | Sun set | Nighttime high tide | (A) Appeared on the beach | Mean time | (B) Entered into the sea | Mean time |
|------------|---------|---------------------|--------------------------|-----------|-------------------------|-----------|
|            |         |                     | n  | Estimate | 95% CI | MRL | p          | n  | Estimate | 95% CI | MRL | p          |
| Jul. 10    | 19:35   | 19:05               | 47 | 20:30    | 20:20–20:43 | 0.984 | <0.001 | 25 | 21:07   | 20:47–21:30 | 0.97 | <0.001 |
| 11         | 19:35   | 19:44               | 31 | 20:23    | 20:15–20:33 | 0.993 | <0.001 | 12 | 21:01   | 20:45–21:21 | 0.991 | <0.001 |
| 12*        | 19:35   | 20:22               | 39 | 20:14    | 20:09–20:27 | 0.993 | <0.001 | 29 | 20:50   | 20:38–21:02 | 0.991 | <0.001 |
| 13         | 19:35   | 21:00               | 20 | 20:12    | 20:01–20:25 | 0.992 | <0.001 | 13 | 20:58   | 20:44–21:14 | 0.993 | <0.001 |
| 14         | 19:35   | 21:38               | 12 | 20:14    | 19:57–20:40 | 0.985 | <0.001 | 9  | 21:25   | 21:07–21:40 | 0.994 | <0.001 |
| Aug. 8     | 19:23   | 18:47               | 16 | 21:20    | 21:01–21:43 | 0.982 | <0.001 | 3  | 20:26   | 20:10–20:40 | 0.999 | 0.0339 |
| 9          | 19:22   | 19:20               | 26 | 21:00    | 20:48–21:13 | 0.991 | <0.001 | 19 | 20:47   | 20:37–20:58 | 0.994 | <0.001 |
| 10*        | 19:22   | 19:54               | 34 | 21:06    | 20:51–21:21 | 0.984 | <0.001 | 12 | 21:02   | 20:41–21:21 | 0.989 | <0.001 |
| 11         | 19:21   | 20:27               | 38 | 21:42    | 21:22–22:00 | 0.968 | <0.001 | 19 | 21:34   | 21:06–22:01 | 0.969 | <0.001 |
| 12         | 19:20   | 21:01               | 21 | 21:30    | 21:13–21:47 | 0.983 | <0.001 | 8  | 21:25   | 21:06–21:37 | 0.995 | <0.001 |
| Sep. 6     | 18:57   | 18:15               | 12 | 20:30    | 20:12–20:47 | 0.991 | <0.001 | 1  | 20:00   | NA         | 1.000 | 0.512 |
| 7          | 18:56   | 18:45               | 44 | 20:03    | 20:33–21:07 | 0.972 | <0.001 | 20 | 20:21   | 20:10–20:31 | 0.995 | <0.001 |
| 8*         | 18:55   | 19:17               | 83 | 21:01    | 20:52–21:10 | 0.983 | <0.001 | 57 | 20:56   | 20:45–21:07 | 0.984 | <0.001 |
| 9          | 18:54   | 19:49               | 78 | 20:33    | 20:19–20:53 | 0.947 | <0.001 | 17 | 20:18   | 20:08–20:28 | 0.996 | <0.001 |
| 10         | 18:53   | 20:21               | 45 | 20:11    | 19:55–20:28 | 0.972 | <0.001 | 19 | 20:24   | 20:08–20:44 | 0.984 | <0.001 |
| Oct. 5     | 18:27   | 17:33               | 2  | 19:00    | NA         | 1.000 | 0.1372 | 0  | NA      | NA         | NA    | NA    |
| 6          | 18:26   | 18:05               | 5  | 19:07    | 19:00–19:15 | 0.999 | 0.0011 | 0  | NA      | NA         | NA    | NA    |
| 7*         | 18:25   | 18:37               | 20 | 19:31    | 19:19–19:45 | 0.992 | <0.001 | 7  | 19:22   | 19:08–19:37 | 0.997 | <0.001 |
| 8          | 18:24   | 19:10               | 29 | 19:24    | 19:18–19:40 | 0.991 | <0.001 | 10 | 19:28   | 19:16–19:40 | 0.996 | <0.001 |
| 9          | 18:23   | 19:43               | 47 | 19:57    | 19:45–20:02 | 0.991 | <0.001 | 20 | 19:56   | 19:45–20:08 | 0.993 | <0.001 |
| 10         | 18:22   | 20:17               | 33 | 19:57    | 19:46–20:07 | 0.991 | <0.001 | 14 | 20:10   | 19:53–20:30 | 0.988 | <0.001 |

*Table 2.* Circular summary statistics of migration of *Coenobita brevimanus* at Amitori Beach during the new moon periods in 2010.

*, new moon; CI, confidence interval; MRL, mean resultant length; n, number of crabs; NA, not applicable; p, Rayleigh test for uniformity.
compressus were very active at night in the intertidal zone patrolling the moist sand in search of food (Herreid & Full, 1986), while the foraging range for beach-living Coenobita, where food and water are co-located, is relatively small (Greenaway, 2003). Inland-dwelling C. brevimanus may also travel extensively, occurring in both coastal forests and along the seashore to search for food during the nighttime; thus, numerous individuals were found through nighttime field surveys in inland areas (Kosuge & Kohno, 2010; Mizutani et al., 2012; Doi et al., 2019) and shores (Fujikawa et al., 2017; present study). Future studies should include confirmation of sex, presence/absence of embryos and spermatophore, and salinity of the store of water in the shells of crabs that are found on the beach in order to further clarify aspects of seaward migration.

The number of crabs crawling on the beach was much larger in the new moon period with higher tidal amplitude than during the full moon with lower tidal amplitude and in other lunar phases. Although seaward migrations were found even in the full moon period, they were highly synchronized to both the new moon (lunar cycle) and the spring tide (semilunar cycle). Timing of reproductive activities in intertidal and supratidal brachyuran crabs has been well studied (Forward, 1987; Morgan, 1995; Christy 2003, 2011), and findings suggest that the most common pattern is for larval hatching to occur at night during high tide on larger-amplitude tides on a bi-weekly or monthly cycle of tidal amplitude (Christy, 2011). Unlike previous studies of larval release of coenobitids on Iriomote Island (Doi et al., 2016, 2018a), tidal amplitudes of the new moon period were higher than those of the full moon period during this study. If tidal cues are more important than lunar cycle in entraining the reproductive rhythm of this species, the rhythm of seaward migration may change when the tidal amplitude is the same extent in both the new and full moon or higher in the full moon period than in the new moon period, (Skov et al., 2005). In coenobitid crabs, the zeitgeber of their reproduction is still unknown, and experimental studies are needed to determine what environmental cues may synchronize larval release.

Unlike the timing of the crabs entering seawater, the timing of the appearance on the beach did not coincide well with high tide but showed several peaks. Earlier and later peaks of appearance may correspond with females releasing zoeae and males mating with females after spawning, respectively. The sexual differences in timing for migration were observed for the Christmas Island red crab (Adamczewska & Morris, 2001) with the timing of immersion coinciding well with the nighttime high tide. Larval release by C. brevimanus occurred in intertidal or subtidal areas near the swash zone and in most cases, larval release occurred immediately after entering seawater (Nio et al., 2014). While C. cavipes release larvae during both flood and ebb tides (Doi et al., 2018a), seawater immersion, i.e., larval release by C. brevimanus almost always occurs during ebb tide with the peak and daily changes in mean time of immersion being within 2 h after the high tide.

The adaptive significance of larval hatching occurring at night during high tide on larger-amplitude tides is believed to be that by moving quickly to the ocean at night, larvae may escape visual detection by planktivorous fishes that are especially abundant in shallow waters (Christy, 2003). Thus, it may be related to species-level differences in life cycle adaptations; i.e., an export vs. retention strategy of larvae (Anger, 2001). The larvae of C. brevimanus and C. cavipes show smaller growth increments, but size of hatching larvae and pelagic duration of larvae are larger and shorter, respectively, for C. brevimanus, and smaller and longer, respectively, for C. cavipes (Hamasaki et al., 2015b). At the present study site, the numerical simulation using a biophysical model
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showed that about 10% of the larvae of C. brevimanus were retained near the spawning site after completion of the larval stage (Murakami et al., 2014). C. brevimanus with its shorter pelagic larval period may promote larval retention near the source population and strict constraint of the timing of spawning compared to the export strategy of C. cavipes. In addition to body size differences, different spination of zoeae between C. brevimanus and other Coenobita (Hamasaki et al., 2014; Kohno et al., 2014) may explain the different larval survival strategies against predation (Morgan & Christy, 1997) among coenobitids.

The zoeal duration of C. brevimanus is 13 to 22 days, and megalopae migrate onto land by around 16 to 18 days after metamorphosis at about 28°C in rearing experiments (Hamasaki et al., 2014, 2015b; Kohno et al., 2014). Therefore, the larval dispersal duration of C. brevimanus is probably 4 to 5 weeks during which more juveniles are expected to be recruited to the coasts in September and October, which is about 1 month after the larval releases. Hamasaki et al., (2018b) investigated the species composition of early juveniles of coenobitids in beaches and river mouth sites on Ishigaki Island from late August to the middle of September. Of a total of 576 early juveniles of five Coenobita species collected, C. brevimanus accounted for only 0.7%. In order to determine the recruitment of the present species, sampling should be performed in autumn at sites near the habitat of adults, such as under logs in the rainforest, in piles of coconut debris (Gross, 1964), at the shore side of dark coastal forest floor, even in daytime (Okinawa Prefectural Board of Education, 1987), in limestone crevices and under the roots of banyan trees (Fujikawa et al., 2017).

Seaward migration of C. brevimanus showed three peaks annually, corresponding to the new moon periods in July to September. Timing of entering seawater, i.e., larval release, coincided well with the new moon and nighttime high tide. This species shows a phenology and rhythm of spawning that is common in coenobitids of the Ryukyu Islands (Imafuku, 2001; Nakasone, 2001; Sato & Yoseda, 2008, 2009; Doi et al., 2016, 2018a). The results of this study are valuable for understanding the population dynamics and structure as well as promoting conservation and management of the near-threatened C. brevimanus in this area along with previous findings from studies using numerical simulation of larval dispersal (Murakami et al., 2014; Doi et al., 2018b), spatiotemporal patterns of recruitment (Hamasaki et al., 2018) and genetic population network analysis with a sensitive genetic marker (Hamasaki et al., 2015a).

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