Spatial distribution, population structure and diel changes in pre-feeding posture of Hippa marmorata (Decapoda: Anomura: Hippoidea) on sandy beaches of Iriomote-jima Island, Ryukyu Islands, in the Western Pacific Ocean

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Abstract.—The spatial distribution, population structure and feeding behavior of the mole crab Hippa marmorata (Hombron & Jacquinot, 1846) was investigated on Iriomote-jima Island, Ryukyu Islands, in the Western Pacific region. Changes in the geographic distribution, body-size distribution, abundance, and vertical migration of mole crabs in response to the circatidal rhythms were examined by sampling sediments using a modified rake. Diel changes in the number of crabs exhibiting a pre-feeding posture to capture zooplankton were examined by visual counts. Mole crabs were more abundant at stations near the mouth of an inlet where terrestrial hermit crabs (Coenobita brevimanus) were previously observed to have released their larvae. The body-size distribution, measured as carapace length (CL), ranged from 5.3 to 20.3 mm in females and 4.1 to 12.1 mm in males. The pre-feeding posture was only observed at night, and increased and decreased in crab numbers observed with the flood (incoming) and ebb (receding) tides, respectively. Regardless of the tidal cycle, mole crabs were only collected in the swash zone, and the number of crabs collected was higher at night. The population structure and tidal migration characteristics of the mole crabs observed in this study closely correspond to the observations of previous studies. The temporal patterns observed in the adoption of pre-feeding posture among mole crabs may be an adaptation to feeding on the zooplankton that typically emerge at night.

Key words: feeding posture, Hippa marmorata, mole crab, spatial distribution

Introduction

Sandy beaches are physically dynamic coastal environments where sand, waves, and tides interact with each other. Consequently, the animals that inhabit these environments are well adapted to substratum instability and the difficulty associated with locating food, as well as the considerable forces associated with wave action. In response to these challenges, sandy-beach macrofauna are typically opportunistic feeders (e.g., filter/suspension-feeding and scavenging) that are highly mobile, good burrowers, and well adapted to life in the swash zone (Brown & McLachlan, 2006).

The anomuran decapod Hippa marmorata (Hombron & Jacquinot, 1846) inhabits tropical and subtropical sandy beaches in the Indo-Pacific region (Osawa et al., 2010). These mole crabs typically burrow into beach sand where they remain in the swash zone by migrating up and down the beach in response to the movement of the tides (Wenner & Fusaro, 1979). However, occasionally mole crabs also aggregate in large numbers on the beach surface (Haley, 1979). The crabs are well known scav-
engers that feed on any carrion that washes up on the shore (e.g., Portuguese man-of-war Physalia physalis) (Bonnet, 1946; Matthews, 1955). Hippa marmorata also adopts a pre-feeding posture in which the animals either fully or partially extend their first raptorial pereopods above the sand surface to feed on mysids and other similar-sized zooplankton by moving the first pereopods toward its mouthpart complex and then out again (Wenner, 1977; Fusaro, 1978; Haley, 1979; Wenner & Fusaro, 1979; Nio et al., 2014).

Nio et al. (2014) reported that some individuals of H. marmorata aggregated around terrestrial hermit crabs (Coenobita brevimanus) and that they may have fed on the larvae that the hermit crab released in the swash zone. Terrestrial crustaceans distributed in coastal areas of the tropics and subtropics exhibit high species diversity and abundance, with most species releasing their larvae directly into the sea (Wolcott, 1988). For the mole crabs, this is a previously unrecognized food source from the terrestrial environment, and is unlike carrion, zooplankton, and macrozoobenthos derived from the sea. Indeed, it would therefore be interesting to accurately clarify the extent to which the mole crabs depend on this mero-plankton, and also to identify the factors responsible for causing mole crabs to aggregate around the hermit crabs. However, very little research has been conducted on plankton-feeding by H. marmorata to date (Wenner, 1977).

Previous studies on the ecology of this species (previously named Emerita pacifica or Hippa pacifica) examined population structure (Haley, 1979; Wenner & Fusaro, 1979; Wenner & Haley, 1981), relationships among food supply, growth, and reproduction (Wenner, 1977; Fusaro, 1978; Wenner et al., 1987), microhabitat selection (Haley, 1982), scavenging behavior (Bonnet, 1946; Matthews, 1955), coloration (Wenner, 1972), and burrowing behavior (Lastra et al., 2002). However, since all of these studies were undertaken on the Marshall Islands and Hawaii, these characteristics are likely to differ markedly from beaches elsewhere (Wenner et al., 1987).

The purpose of this study is therefore to clarify the changes in spatial distribution, population dynamics, and plankton feeding in H. marmorata with respect to diurnal and tidal cycles in the Western Pacific region in order to determine its geographical variation. This was accomplished by collecting samples and conducting visual observations at different times under different tidal conditions on the sandy beaches of Iriomote-jima Island in Okinawa, Japan.

Materials and methods

Study area and sampling stations

The study area, Amitori-wan, consisted of an inlet measuring 2.3 km wide and 3.5 km along the northwestern coast of Iriomote-jima Island in the Ryukyu Islands in the Western Pacific region (Fig. 1). The inlet opens into the East China Sea in the north and receives runoff from two streams in the south. The annual sea surface temperature at the inlet ranged from 16.7 to 32.3°C in 2013 (mean ± SD, 25.2 ± 2.8, N = 52028), recorded at 10-minute intervals using a water temperature data logger Tidvit v2 (Onset Computer Cooperation). The coastline of the inlet is primarily composed of rocky
spatial distribution and feeding posture of Hippa marmorata

Shores. The sampling stations were located on 10 separate sandy beaches, each measuring 50 to 350 m, to the west (W1–W5) and east (E1–E5) of the inlet mouth. Sampling stations were further subdivided into 1 to 5 substations, each measuring 50 m in length, that were numbered in numerical order from the mouth of the inlet in the north to the head of the inlet in the south. The bottom habitat of each station was medium or coarse sand, while, at substation W1-7, the sediments included coral rubbles around level of the extreme low water of spring tide.

**Sampling methods**

The sampling equipment used in this study consisted of a modified rake for collecting specimens. The rake was fitted with a basket (50 cm wide, 20 cm high, 30 cm deep) and a handle (100 cm long), all of which were made of steel. The side and bottom of the basket were covered by 5 mm steel mesh, and the bottom of the opening was lined by a row of triangular teeth (45 mm high, 48 mm long) to facilitate the collection of crabs. The sediments were raked by pulling the rake backwards (vertically against the shore) over the sand for a distance of 1 m to collect a consistent amount of sediment at a depth of approximately 5 cm. At any one substation, raking was repeated 5 times, with each swathe 5 m away from the previous one in a horizontal direction, moving from the opening of the inlet to the head of the inlet. The crabs were then separated from the sediments in the rake basket, identified to species, and then returned to approximately the same location as where they were captured.

**Crab distribution within Amitori-wan inlet**

The distribution of H. marmorata within the Amitori-wan inlet was investigated for the two hours before and after high tide during the daytime on 25 June and 6–10 July 2013. Sampling using the rake was performed in the swash zone (at the upper extent of the wave wash) during the backwash of waves at 10 stations (41 substations).

**Body-size distribution**

The size distribution of mole crabs was recorded at stations W1, W2, E1, and E2 during the daytime and nighttime on 5–7 and 10 July 2013. The crabs in the swash zone were collected using the rake as described above. For each individual crab, carapace length (CL; mm), sex, and the presence or absence of embryos attached to the pleopods, were recorded immediately before the crabs were returned to the beach. The CL histogram of each sex was modeled as a mixed normal distribution using mclust package (Fraley & Raftery, 2003; Fraley et al., 2012) in R version 3.0.2 (R core team, 2013). The parameters (mean, SD, and mixing probabilities) of each normal distribution were estimated by expectation-maximization algorithm. The number of normal distributions can be estimated by maximizing the Bayesian Information Criteria.

**Diel changes in the number of crabs exhibiting pre-feeding posture**

Mole crabs exhibiting a pre-feeding posture (Matthews, 1955; Wenner, 1972; Nio et al., 2014) were counted with the naked eye by the same investigator for a 10 min period every hour from 21:00 (Japan Standard Time) on 23 July to 21:00 on 24 July 2013. These observations were conducted in the 5 m-wide swash zone at two substations where the crabs were most abundant (W1-6, W1-7, see Results). A red headlamp was used to conduct observations at nighttime so as not to disturb the nocturnal behavior of the mole crabs. The calm weather conditions on the nights when observations were conducted meant that the crabs and the V-shaped ripples created by their bodies in the outgoing wave swash could be easily observed.

**Abundance of burrowing mole crabs in the swash zone**

The abundance of mole crabs in the swash
zone at stations W1 and W2 was examined using the rake one hour before and after the high tide during the daytime and nighttime on 5 and 10 July 2013.

**Vertical and longitudinal distribution of crabs in response to circatidal changes**

Mole crab abundance in the surf zone was examined at different phases in the tidal cycle by raking during the daytime and nighttime at substation W1-7. Sampling performed in the emersed, swash, and immersed zones (five replicates in each zone) at different phases in the tidal cycle, i.e., high tide (HT), low tide (LT) and at the midpoint between HT and LT (MT). The temporal order of the surveys was as the tide was receding from HT to LT (ebb tide) on 5 August 2013 and in the reverse order (flood tide) on 6 and 7 August 2013.

**Results**

**Crab distribution in the Amitori-wan inlet**

A total of 178 individuals of *H. marmorata* and a single specimen of *H. adactyla* were collected during the distribution survey. Mole crabs were most abundant (mean >1 crabs per five rakes) at the stations near the mouth of the Amitori-wan inlet (W1, W2, and E1; Fig. 2). Relatively fewer mole crabs were collected at the other stations, particularly at the stations closest to the head of the inlet, such as at W4, W5, E4 and E5 (Fig. 1).

**Body-size distribution**

The size distribution of individuals collected in this study ranged from 4.1 to 12.1 mm CL for males (mean ± SD, 8.14 ± 1.4), 5.3 to 20.3 mm for females (mean ± SD, 12.2 ± 2.9), and 7.4 to 20.3 mm for ovigerous females (mean ± SD, 12.9 ± 2.4) (Fig. 3). The 95th percentile of CL was 10.6 for males and 16.6 for females. The 5th percentile of CL for ovigerous females was 9.19 mm. The size-frequency distributions differed between the sexes (Kolmogorov–Smirnov test, $D = 0.7077$, $P < 0.001$). The size frequency distribution of males was best fitted to a univariate normal with one component model, while in females to a univariate, unequal variance with two components model. The parameter (mean ± SD of CL and number of females) of two normal distributions was estimated to 6.9 ± 0.38 (15 females) and 12.6 ± 2.55 (143 females). The

![Fig. 2. Abundance of Hippa marmorata at each substation in Amitori-wan inlet. Bars and error bars show the mean and standard error of the number of individuals collected using a rake (five replicates), respectively.](image-url)
proportion of ovigerous females was 60%.

**Diel changes in the number of crabs exhibiting pre-feeding posture**

Mole crabs only exhibited the pre-feeding posture at nighttime, and followed a temporal rhythm associated with the tidal cycles (Fig. 4). Specifically, the number of individuals observed at both of the stations surveyed (St. W1-6 and W1-7) decreased gradually after peaking at high tide just after dusk, before reaching the lowest levels at low tide at midnight and then peaking again just before dawn. Most of the crabs were oriented towards the sea.

**Abundance of sand-burrowing mole crabs in the swash zone**

The number of crabs collected per raking was higher at nighttime than during the day (Fig. 5). At substations W1-6, W1-7, and W2-1, where numerous crabs were collected, more than approximately 4 crabs per rake swathe were collected at nighttime, which is almost twice that collected during the daytime. The maximum and minimum number of crabs collected at each station exhibited the same tendency in both periods (Paired t-test, $t = -3.08$, $P = 0.996$).

**Vertical and longitudinal distribution in response to circatidal changes**

Except for during low tide in the daytime, only 1 to 3 mole crabs were collected in the swash zone irrespective of successive tides and circadian phases (Fig. 6). At substation W1-7, the substratum at a point 30 m from the mean high water mark contained a high proportion of pebbles and broken corals, which meant that no crabs were collected at this site at low tide during the daytime.

**Discussion**

The density of *H. marmorata* was higher at the stations near the mouth of the inlet (Fig. 2). This species is a passive feeder, which scavenge carrion that washes up onto beaches.
from the open ocean (Matthews, 1955; Wenner, 1977) and on zooplankton that washes ashore at night (Wenner, 1977). In addition, *H. marmorata* is also a sediment generalist and has a distribution that is not limited by sediment size (Lastra et al., 2002). Rather, the distribution of this species is considered to be affected by the ease with which prey and carrion can be locat-
ed. Within the Amitori-wan inlet, the distribution of mole crabs was observed to correspond with the distribution of the sites used by the terrestrial hermit crab *C. brevimanus* to release larvae (Mizutani & Kohno, 2012). The phenology underlying the release of larvae by *Coenobita* crabs (summer breeding) is restricted to particular sites along the shore (Wolcott, 1988; Imafuku, 2001), and the phenology is a predictable event that is governed by lunar and tidal cycles (Nakasone, 2001). However, it is not yet known whether *H. marmorata* aggregates at these sites in order to feed on the *Coenobita* larvae that are being released (Nio et al., 2014) in spatial scale within the inlet, or whether the selection of the same sites is a coincidence, arising from both taxa employing similar hydrologic and/or topographic cues to aggregate and release larvae, respectively. Our ongoing distribution study performed in longer time scales including non-breeding season for *Coenobita* crabs may help examine this correspondence.

The 95th percentile of CL for males (10.6 mm) from the Amitori-wan inlet corresponds with measurements obtained at Enewetak in zones where food is scarce (mean ± SD of 95th percentile of CL for males, 12.2 ± 1.0 from 18 samples (days) at 8 sites in various seasons) and intermediate (13.01 ± 0.78 from 28 samples at 7 sites) (Wenner et al., 1987). That of females (16.6 mm) from the Amitori-wan inlet corresponds with measurements obtained at Enewetak in zones where food is scarce (16.3 ± 1.9) (Wenner et al., 1987). The increase in the maximum size attained by males and females likely depends on a stable food supply (*e.g.*, zooplankton) (Wenner et al., 1987). Therefore, at Amitori-wan inlet, the maximum CLs for males and females were smaller than those at Enewetak in zones where food is rich (13.4 ± 0.6 for males and 19.7 ± 1.6 for females in 95th percentile of CLs from 18 samples at 6 sites), possibly due to food scarcity. The population of *H. marmorata* examined in this study seems to be composed of one and two cohorts in males and females (Fig. 3). This result may be attributed to differences in the growth rate, because males cease molting before females and therefore stop growing (Wenner & Haley, 1981).

The 5th percentile of CL for ovigerous females (9.19 mm) was considerably smaller than that observed at Enewetak (mean ± SD of 5th percentile, 11.9 ± 1.3 in food poor zones) (Wenner et al., 1987) and Hawaii (mean ± SD of minimum, 13.6 ± 0.8 mm) (Haley, 1982). A sudden increase in food availability (*e.g.*, a marked increase in carrion, such as *Physalia* in Hawaii) has been shown to result in a dramatic and marked increase in the proportion of ovigerous females (Wenner, 1977; Fusaro, 1978), but it has a less dramatic and delayed effect on the body size at onset of egg production (*i.e.*, the 5th percentile or minimum size of ovigerous females) (Wenner et al., 1987). Thus, other than differences in long-term food supply, the factors affecting the geographical variation of size at maturity in this species have not yet been clarified. However, other possible factors (*e.g.*, temperature, temporal changes) could not be considered due to the time constraints of the present study (only July).

The pre-feeding posture exhibited when feeding on zooplankton was only observed at nighttime (Fig. 4). In surveys conducted during the daytime, the number of crabs per rake swathe decreased as the mole crabs burrowed deeper into the substratum of the wash zone (Figs. 5 and 6), as is observed by Shepherd et al. (1988). The adoption of this posture by the mole crabs was observed to have two peaks; one at midnight and another immediately before dawn (Fig. 4). These peaks corresponded with the emergence of potential prey, such as zooplankton (Saigusa & Oishi, 1999), and the release of larvae by terrestrial crustaceans (Sawamoto et al., 1988; Nakasone, 2001). Thus, it is suggested that the temporal pattern

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observed in this pre-feeding posture might be adaptation to the nocturnal emergence of zooplankton. During the daytime, the mole crabs that burrow into the sand and do not exhibit this pre-feeding posture as the abundance of prey is relatively low (Saigusa & Oishi, 1999), and the risk of predation by predators such as birds and fishes is high. However, when carrion is washed up on the beach, the mole crabs may emerge from the substratum to scavenge, even during the daytime (Bonnet, 1946; Matthews, 1955).

The distribution of _H. marmorata_ changed over a longitudinal distance of 30 m in the wave wash zone during the incoming and receding tides, both during the daytime and nighttime (Fig. 6). This semi-diurnal tidal migration pattern corresponds with the general migration patterns observed in conspecific populations in Hawaii (Haley, 1982) and congeneric populations on Barbados Island (Hanson, 1969) and in western Australia (Shepherd et al., 1988). The distribution of the crabs examined in this study thus changed with the fluctuations in the tide (Fig. 6), and no crabs were observed during the daytime (Fig. 4, 5). These findings suggest that _H. marmorata_ undertakes longitudinal and vertical movements in the sand column in the daytime and that these migrations are synchronized with the tidal cycle.

This study has clarified diel changes in feeding behavior, habitat utilization, and population structure of _H. marmorata_ on a Western Pacific island. It appears that the circatidal rhythms of pre-feeding posture and the distribution of _H. marmorata_ within the inlet are adapted to feed on the influx of zooplankton at high tide and the release of larvae by terrestrial crustaceans. In sandy beach environments, physical forces have a marked effect on the movements of mobile animals, but other phenomena (such as visual cues or chemical stimuli, including pheromones) may also be important (Brown & McLachlan, 2006). Indeed, the existence of a casual relationship between mole crab aggregations and the release of larvae by hermit crabs may be an example of such a phenomenon, _i.e._, visual cues and/or chemical stimuli. Further studies should therefore be conducted to better clarify these points and increase our understanding of the feeding habits of _H. marmorata_.

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