Distribution, size structure, and relative growth of *Epigrapsus politus* (Brachyura: Gecarcinidae) in a subtropical bay in Japan

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**Abstract.**—The distribution and population characteristics of the land crab *Epigrapsus politus* were studied in the Amitori Bay, Iriomote-jima Island, Japan. The crabs were most abundant on the western coast of the bay, particularly at the stations near the tip of the peninsula, where stranded carrion or algae often accumulate. *E. politus* was found only above the extreme high water of spring tide, where more cobbles and pebbles were piled by the waves. The carapace width (CW) of the individuals ranged from 6.94 to 21.94 mm for males (*n* = 98) and from 9.83 to 19.98 mm for females (*n* = 75). Because the population showed a polymodal length frequency or multiple modes, the lifespan was estimated to be at least two years. Adult males showed progressive polymorphism in chelae, and the proportion of heterochelous males and the size difference between major and minor chelae increased with increase in CW. The puberty molt brought about changes in the relative growth rate of the major chela in the males and the abdomen in the females. The size at 50% morphometric maturity was estimated to be about 14 mm CW and corresponded to the CW at about one year of age.

**Key words**: Iriomote-jima, land crab, Ryukyu Islands, Yaeyama Islands

**Introduction**

Gecarcinidae H. Milne Edwards, 1837 is a family of semi-terrestrial brachyuran crabs that are generally referred to as “land crabs.” There are only seven genera of these crabs worldwide (Guinot *et al.*, 2018). However, these crabs are abundant and dominant members of crab fauna in inlands and continental maritime coast of the tropical and subtropical regions (Green 1997; Sherman 2002; Lindquist *et al.*, 2009). The body-size of most gecarcinid species is medium to large, and the carapace width of some species exceeds 100 mm (Bliss, 1968; Hartnoll *et al.*, 2010). They have smooth and swollen carapaces that are strongly convex, with entire or almost entire anterolateral margins (Ng, 2002). Post-settlement gecarcinid individuals are found in various terrestrial habitats and the level of terrestriality varies substantially among genera. They can be divided into some groups by general appearance and/or the habitat environment where they reside (Türkay, 1987). Species of the genera *Johngarthia*, *Gecarcinus*, and *Gecarcoidea* are the most terrestrial group (Hartnoll, 1988). The genera *Cardisoma* and *Tuerkayana* form a second group, whose habitat is less terrestrial as they are generally frequent in mangrove fringes or swampy areas (Hartnoll, 1988; Guinot *et al.*, 2018). A third group, formed by species of the genus *Discoplax*, are long-legged and cavernicolous (Guinot *et al.*, 2018).

The genus *Epigrapsus*, forms a fourth group consisting of two species (Naruse *et al.*, 2018). Members of *Epigrapsus* are relatively smaller and flatter than members the other genera of gecarcinids (Ng, 2002). Earlier studies have focused on *E. notatus*. Their population biology, reproductive season, lunar entrainment of lar-
val release, relative growth, and butch fecundity has been studied in Taiwan (Liu & Jeng, 2005). The second species \( E. \) politus has been poorly studied and is the target species of this study. It is widely distributed eastward from the Andaman and Nicobar Islands along with \( E. \) notatus (Türkay, 1974). Previous studies on the biology of \( E. \) politus focused on the morphology of the first zoea (Cuesta et al., 2002), the chelar growth of adult males (Hartnoll et al., 2017), and their reproductive season in Taiwan (Liu & Jeng, 2005; as an unpublished data of the paper on \( E. \) notatus). The distribution of this species in Japan was first reported by Ng et al. (2000) based on samples collected from Ishigaki-jima Island. Thereafter, reports of occurrence with brief notes on their habits and ecology were reported from the Okinawa-jima Island (Osawa & Fujita, 2005), Amami-Ohsima Island (Suzuki et al., 2008), and the Miyako Island Group (Fujita & Sunagawa, 2008; Fujita, 2009, 2017). \( E. \) politus inhabits the supralittoral zone, under small partially embedded stones in sandy areas, covered partially by coastal vegetation, including \( Casuarina \) trees (Ng et al., 2000). Among the Gecarcinids, \( E. \) politus reside in habitats nearest to the seacoast and are expected to have exceptional ecological aspects.

Since the coastline of Okinawa Island remained in a natural state in 36.8% of its surface area, but others zones were land-filled or armored (Masucci & Reimer, 2019), the sandy beach with the embedded stones where \( E. \) politus inhabit are limited and may decrease in the future. To conserve this species, quantitative ecological information such as habitat requirements, density, and reproductive parameters are indispensable. However, our current knowledge of this species is largely confined to their taxonomy and geographic distribution. Hartnoll et al. (2017), only published an article for post-settlement ecology of \( E. \) politus, where they showed that chelae polymorphism was found in males, photographed the two types of chelae, and showed that the proportion of marked heterochelous males increased in larger body sizes. Relative growth of male chelar size is frequently analyzed for estimating the functional maturity size (Hartnoll, 2012), but Hartnoll et al. (2017) did not focus on the size at maturity and they analyzed only 57 males collected in Moorea and some deposited specimens.

In this context, the purpose of this study was to clarify the distribution and habitat, the size structure, and morphological size at maturity of \( E. \) politus on a sandy beach along a small subtropical bay for a better understanding of its ecological aspects. This was accomplished by designing and undertaking semi-quantitative sampling and analyzing the relative growth of these samples collected from the Iriomote-jima Island, Okinawa, southern Japan. Since Hartnoll et al. (2017) was published after our survey of this study was finished, we did not focus on the changes of morphology of chela. However, we obtained morphometric data for more males and therefore discuss chelae polymorphism.

Materials and Methods

Distribution

The study was undertaken in the Amitori Bay, in the supralittoral zone where stones are embedded in the sandy beach. The width of the study site was 2.3 km and the length was 3.5 km along the northwestern coast of Iriomote-jima Island \((24^\circ24'N, 123^\circ46'E)\) (Fig. 1), one of the southern Ryukyu Islands, Japan. Because \( E. \) politus inhabits sandy areas with small, partially embedded stones in the supralittoral zone (Ng et al., 2002), 37 study stations in areas with cobbles were selected along the coastline of the Amitori Bay to study the horizontal distribution of this species. At each station, crabs were collected within two 1 m² quadrats. Sampling was undertaken over eight days, between July 23 and August 21, 2017: St.
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1–6 (21 August), St. 7 (23 July), St. 8–12 (6 August), St. 13–20 (7 August), St. 21–26 (8 August), St. 27–32 (9 August), and St. 33–37 (20 August). Within each quadrat, stones were turned over and removed, and any *E. politus* present on the base substrate or on the stones were collected by hand or by using a forceps. The stations were divided into five groups (outer west, inner west, innermost, inner east, and outer east) based on the topography of the study area (Fig. 1).

**Vertical distribution**

The cobble area of St. 6 was chosen as the site at which vertical distributions were studied, because of the high density of *E. politus* that was recorded here (second highest). St. 6 was easier to access compared to the densest area (St. 5). The station was gridded into 104 cells measuring 1 m × 1 m (Fig. 2; 1–6 rows × A–R columns), and the crabs were collected from each grid between 5 and 8 September following the same method as that used in the distribution study. The extreme high water of spring tide (EHWS) was the boundary between the rows 3 and 4, 2 and 3, and 1 and 2 of the

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Fig. 1. Map of and Iriomote-jima Island (inset) and location of Amitori Bay (arrow), and sampling stations (1–37) along the bay (Map source: Geospatial Information Authority of Japan).

Fig. 2. 104 grids (1 m × 1 m) of the Station 6 (see Fig. 1). The oblique lines indicate the area below the extreme high water of spring tides. The crosses indicate grids that were not sampled due to a lack of sediments (A1, P1, Q1, and R1).
columns A–J, N, and O–R, respectively. EHWS reached a third of the height in K3–M3. St. 6 was covered by a flaring shaped seawall with a gentle slope.

**Measurements**

All measurements were made on living animals in the field. Crabs were sexed according to the morphology of the abdomen and the females were further noted as bearing non-eyed or eyed eggs. All individuals were then measured for carapace width (CW). The right and left cheliped propodus height (just proximal to the insertion of the dactylus, RChH, LChH) for the males, and the abdominal width measured on the fourth abdominal segment (AW) for the females were measured to the nearest 0.01 mm using a Vernier caliper. In order to analyze polymorphism of chelae and the relative growth, the samples collected in a mark-recapture experiment at St. 6 between September and November 2017 (Doi et al., unpublished data) were additionally included in the analysis.

**Statistical analysis**

All statistical analyses were performed using the R version 3.4.3 (R core team, 2017) with a 5% significance level. To determine the population size structure, the CW histogram of each sex was modeled as a mixed normal distribution using mclust function in the mclust package (Scrucca et al., 2016). The parameters (mean, standard deviation (SD), and mixing probabilities) of each normal distribution were estimated by the expectation-maximization algorithm. The number of normal distributions was estimated by maximizing the Bayesian Information Criteria.

The CW of each station was compared across the four topographic groups with the exception of the innermost stations (Fig. 1; see results) using one-way ANOVA followed by the Tukey–Kramer post hoc test. The number of crabs collected from each row at St. 6 was modeled using a negative binominal generalized linear model (GLM) with logit-link by using the glm.nb function in the package MASS (Venables & Ripley, 2002). In this analysis, the number of crabs per grid was the response variable, and the number of rows represented the categorical variable.

The mature males of *E. politus* showed homo- or heterochely (Hartnoll et al., 2017). The heterochely ratio (HR) of chela height was calculated as the chela height of the major cheliped (MChH, the larger of RChH and LChH) divided by that of the minor cheliped, and the Type A and Type B males had HR ≤ 1.1 and > 1.1, respectively (Hartnoll et al., 2017). A generalized linear mixed-effects model (GLMM) with binomial family (logit-link) was used to determine whether the cheliped heterochely and handedness change with CW. In these analyses, the proportion of heterochely (0: Type A; 1: Type B) and right-handedness were binary response variables, CW represented the numerical explanatory variable, and the effect of the individual crab was considered a random effect.

Analysis of the relative growth of MChH and AW (response variables) to CW (explanatory variables) was performed using the function classify-mature in the package sizeMat (Torrejon-Magallanes, 2018) for determining the morphological size at sexual maturity. A principal components analysis (PCA) was conducted with two allometric variables (CW vs. MChH and CW vs. AW) in log base, which allowed distinguishing two groups that would represent morphological immature and mature individuals. Individuals were assigned to these two groups according to their loads on the two axes of the PCA (Corgos & Freire, 2006). Using the results of the classification (PCA + cluster), a linear discriminant analysis was carried out to obtain a discriminating function. The size at 50% morphometric maturity ($L_{50}$) was estimated using a logistic regression with CW and ma-
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Results

Distribution

A total of 181 individuals of *E. politus* were collected during the distribution survey. The crabs were most abundant at the stations on the western coast of the bay, particularly at the stations near the tip of the peninsula, such as at St. 5 and 6 (Fig. 3). Relatively fewer crabs were collected at the eastern stations (St. 21–37) and there were no crabs collected at the stations on the innermost part (St. 16–20).

Size structure

The size of the individuals collected in Amitori Bay ranged from 6.94 to 21.89 mm CW for males and from 10.72 to 19.41 mm for females (Fig. 4). A single component model was best fitted to both males and females and the CW showed normality in both males (Shapiro–Wilk test, W = 0.982, p = 0.189) and females (Shapiro–Wilk test, W = 0.969, p = 0.067). The mean CW for males (Mean ± SD = 15.64 ± 3.15 mm, n = 98) differed significantly from that of the females (Mean ± SD = 14.81 ± 2.27 mm, n = 75; Welch’s t-test, t = 2.021, df = 170.4, p < 0.05). Unlike the result of model fitting, the length frequencies of the males showed three peaks (12.0–12.9, 14.0–15.9, 19.0–19.9 mm) with two individuals that were much smaller. The length frequencies of the females also showed multiple peaks, and the bins 11.0–11.9, 13.0–13.9, and 18.0–18.9 mm were clearly recognized. The CW of an ovigerous female with non-eyed eggs was 14.1 mm.

Although the modes and mean CW of males...
differed with the topography, it was significantly different only between the outer and inner western stations (Fig. 5; Tukey–Kramer post hoc test, \( p < 0.001 \)). No significant differences were found for the females (ANOVA, \( F_{3, 71} = 1.4, p = 0.25 \)).

**Vertical distribution**

The crabs were collected only above the maximum water line of the spring tide at rows 1–3 and none was collected at rows 4–6 at the higher intertidal zone (Fig. 6; \( n = 93 \)). The negative binominal GLM showed that the number of crabs collected decreased significantly in the lower rows (rows 2 and 3) at St. 6 (Table 1).

**Relative growth and morphological size at maturity**

Of the 301 males that had both chelipeds,
116 were Type B (>1.1 HR), 21 and 10 males had lost the left and right chelae, respectively. The GLMM applied to the cheliped polymorphism data revealed that the proportion of Type B males increased with CW (Fig. 7; Table 2). The proportion of right-handed Type B males did not significantly increase with CW (Fig. 8; Table 2). The HR of Type B males was significantly different between the CW categories (Fig. 9; Fisher’s exact probability test, \( p < 0.001 \)). HR of Type B males ranged from 1.10 to 2.35 and they were divided into three categories; smaller (HR≤1.5), medium (1.5<HR≤1.9), and larger (1.9<HR). There were no males with either medium HR or larger HR at the smallest CW (≤12 mm), but the proportion of males that had medium HR gradually increased with CW and reached 50–70% at the 16.01–20.00 mm CW class. Males having larger HR were found in the 16.01–20.00 mm CW class and not in the largest CW class. The proportion of males with larger HR was highest at the 16.01–18.00 mm, but this was less than 20%.

The onset of sexual maturity in males was associated with significant changes in the relative growth of MChH (Fig. 10A). The PCA classified immature and mature groups (Fig. 10B) and the linear regressions of were as follows:

**Table 2.** Results of binominal generalized liner mixed-effect models examining (A) the proportion of heterochely (Type B males) and (B) proportion of right-handed males of *Epigrapsus politus* (\( n = 332 \)) in Amitori Bay

| Response variables | Coefficients | Estimates | Standard error | \( z \) | \( p \) |
|--------------------|--------------|-----------|----------------|------|------|
| (A) Proportion of Type B | Intercept | -2.527 | 0.670 | -3.769 | 0.0002 |
| | Carapace width | 0.134 | 0.042 | 3.216 | 0.0013 |
| (B) Right-handed | Intercept | 0.053 | 1.011 | 0.052 | 0.9580 |
| | Carapace width | 0.001 | 0.061 | 0.160 | 0.8730 |

![Fig. 7](image1.png) Relationship between the proportion of heterochely (0: Type A; 1: Type B) and carapace width (CW) in male *Epigrapsus politus* in Amitori Bay. The solid and broken curves are logistic equations for the proportion of heterochely against CW and their 95% confidence intervals, respectively.

![Fig. 8](image2.png) Proportion of right- and left-handed individuals of each carapace width size class in heterochelous male *Epigrapsus politus* in Amitori Bay. The numbers in each column indicate sample size.
\[ MChH = 0.109 + 0.622\, CL \text{ for immature males (}\ n = 93), \]
\[ MChH = -1.916 + 0.753\, CL \text{ for mature males (}\ n = 208). \]

The slopes of these lines were significantly different (ANCOVA, \( F_{3,208} = 960, p < 0.001 \)). The logistic function of the proportion of individuals that were mature (PM) was estimated by the GLM as follows:

\[
PM = \frac{1}{1 + \exp \left[-(-31.293 + 2.301 \cdot CW)\right]},
\]

and \( L_{50} \) (mm) was estimated to be 13.6 with 13.4–13.8 95% confidence interval (CI) (Fig. 10c).

The sexual maturity in females was accompanied only by a change in AW in proportion to CW (Fig. 11A). The PCA classified immature and mature groups (Fig. 11B), and the relative growth of AW against CW in females was fitted as follows:

\[
AW = -1.483 + 0.711\, CW \text{ for immature females (}\ n = 106),
\]
\[
AW = 0.475 + 0.595\, CW \text{ for mature females (}\ n = 180).
\]

The slopes of these lines were significantly different (ANCOVA, \( F_{3,282} = 1083, p < 0.001 \)). The logistic function of PM was estimated by the GLM as follows,
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Fig. 11. Relative growth of the width of the fourth abdominal segment against carapace width (CW) (A), principal component analysis scores for the classification of morphological maturity (B), and proportion of maturity against CW (C) of female *Epigrapsus politus* in Amitori Bay. The solid curves and shaded region in C are logistic equations for the proportion of maturity against CW and their 95% confidence intervals, respectively.

\[
PM = \frac{1}{1 + \exp \left[ -(-95.285 + 6.688 \cdot CW) \right]},
\]

and \(L_{50}\) (mm) was estimated to be 14.3 (14.1–14.3 95% CI) (Fig. 11C).

**Discussion**

**Distribution**

In Amitori Bay, the density of *E. politus* was higher at the stations near the mouth, on the western side of the bay (≥10 at St. 2, 4, 5–8). At St. 6, where most of the *E. politus* were collected, mats of seaweed (*Sargassum* spp.) and other terrestrial plant materials such as driftwood were found after the typhoons which approach Iriomote-jima Island between July and September (Doi *et al.*, pers. obs.). The distribution found in *E. politus* corresponds to that of the mole crab *Hippa marmorata*, which feeds on stranded carrion that washes up on the shore at the study site (Suguri *et al.*, 2015). Although the feeding habits of *E. politus* are still unknown, the stranded carrion or other materials may be a direct or indirect food source for this species. In Iriomote-jima Island, the most frequent wind direction is towards the south between May and August, but in other months, it is towards the north-east. Therefore, it is expected that more drift materials are washed ashore on the western coast of the Amitori Bay and this probably contributes to the higher density and the larger body size through fast growing and higher survival rate of *E. politus* found there.

There were no *E. politus* collected below the EHWS in St. 6. At the intertidal zone, the cobbles and pebbles are moved by the waves and their habitat seems to be disturbed frequently. At St. 6, the seawall was constructed behind the habitat of *E. politus*; therefore, more cobbles and pebbles are piled by wave action above the EHWS at the rows 1–3 rather than at the other stations. The piled stones probably increased the habitat structural complexity and this may have contributed to the higher density and the larger body sized crabs (increase in molting individuals) found above the EHWS (Beck, 1995).

**Size structure**

*E. politus* (6.94–21.89 mm CW for males
and 10.72–19.41 mm CW for females) was found to be smaller in size structure than E. notatus, which measured 22.0–36.4 mm for males and 16.9–34.8 mm for females (Liu & Jeng, 2005). Length frequencies of CW were fitted to a single normal distribution for males and females, but they showed several modes, and smaller and larger groups were visually distinguished around 14–16 mm CW. The presence of various sized groups shows that there were multiple year classes of E. politus and the longevity is estimated to be at least two years, because recruitment should occur within a shorter time as the annual breeding period is restricted (August-October; Liu & Jeng, 2005; September-November; Doi et al., unpublished data). The smaller maximum size and narrower CW frequency distribution for females were due to the lower investment in somatic growth and their limited growth during incubation. Female crabs divert a major part of their energy to the ripening of ovaries and cannot molt whilst incubating eggs (Hartnoll, 2006).

**Heterochely and relative growth**

Sexual chelar dimorphism is a common characteristic in gecarcinids (Hartnoll, 2012). Predictably, the degree of sexual dimorphism is very marked in E. politus. Causal factors of cheliped dimorphism of male Epigrapsus include, in the order of most possible to least possible, progressive polymorphism (the switch to heterochely occurring in some small mature males), definitive polymorphism (shift to the mature morphs at the puberty molt), and cheliped loss and its regeneration (Hartnoll et al., 2017). The present study examined 301 males covering the entire size range and showed that both the proportion of heterochelous males and their HR increased with CW, but the proportion of right- and left-handed crabs did not change ontogenetically. These facts also strongly suggest that E. politus is homochelous innately but the difference between major and minor chelae becomes obvious due to the switch from homochelous to heterochelous after the puberty molt. There is no preferential handedness in E. politus, similar to other gecarcinids (Hartnoll et al., 2017), suggesting that handedness is randomly determined as in the case of Uca lactea (Yamaguchi, 1977). However, both this study and that of Hartnoll et al. (2017) did not reject the possibility of definitive polymorphism and cheliped regeneration. Observations of puberty molting of males and an experiment of removal chelipeds are needed to further clarify the chela development and polymorphism.

This study revealed increases in the growth rate of MChH of males and decrease in that of AW of females, relative to CW in E. politus after puberty. Large chelipeds are often important in males because they are associated with combat, display and courtship of potential mates (Hartnoll, 1974). Lower relative growth rate of AW after the puberty molt is seen in E. politus, which is similar to other female gecarcinid (Hartnoll et al., 2006; Shiozaki-Mendes et al., 2013). For female crabs, changes of relative growth rate were found in AW, which grew positively and negatively before and after maturity, respectively, and increased abruptly at maturity. This pattern of morphological change also agrees with the general pattern for brachyuran females (Hartnoll, 1974).

The L₅₀ for both sexes, based on the relative growth analysis, was approximately the boundaries of the groups with smaller CW and larger CW of the respective sex. Because the smaller size groups are likely to correspond to the previous year’s recruitments, the age at sexual maturity for E. politus may possibly be one year. This needs to be confirmed by studying the absolute growth of E. politus.

**Conclusion**

This study revealed the distribution, habitat, body size structure and size at morphological maturity of E. politus, a poorly studied species. The sandy beaches, the habitat of E. politus,
have been threatened and there is a natural coastline decreased (Defeo et al., 2009; Massucci & Reimer, 2019). The high density of *E. politus* in an environment surrounded by artificially placed cobbles and seawalls (St. 6) is a hopeful fact for the conservation of crabs that inhabit such cobble shores. The relative smaller-sized body and smaller size at sexual maturity of *E. politus*, compared to other gecarcinids with larger-sized body and larger size at sexual maturity (e.g., Hartnoll et al., 2006, 2007, 2009; Liu & Jeng, 2007), helps it adapt to unstable environments such as cobble shore. Attaining sexual maturity in shorter time may contribute to a quick recovery of declined population. The distribution found in this study is just a snapshot on a single summer month and the causal factor of chelar polymorphism still remains unclear. Future study should help elucidate these points and provide an integrative view of the ecology of *E. politus*.

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