Growth analysis and population size estimation of coconut crabs based on a large recapture dataset

Shin-ichiro Oka, Koji Tokutake, Tadanobu Inoue

Abstract.—Growth analysis and population size estimation of the northernmost population of coconut crabs inhabiting Ocean Expo Park, Okinawa, southern Japan, was performed using the fishmethods package on R software. In this study, we used more than 500 datasets obtained from the mark-recapture surveys conducted during 2006–2019. We also obtained 126 datasets from our previous study, which was performed using the same field protocol and manual data calculation. The generated data of growth parameters in the GROTAG model were similar to those of a previous study that calculated parameters manually using smaller datasets, and the results obtained were more accurate. To our knowledge, this is the first time that mark-recapture data were used for estimating the population size of coconut crab. The results showed that 1045 individuals (93.3/ha) inhabited the park. This indicates that despite certain environmental disadvantages in the northernmost area, the population density of coconut crabs in this region is not low compared to that at other locations.

Key words: robber crab, mark-recapture, GROTAG, Schnabel method

Electronic supplementary material. The online version of this article contains supplementary material at https://www.jstage.jst.go.jp/article/crustacea/50/0/50_145/_article

The coconut crab, *Birgus latro* (Linnaeus, 1767), is widely distributed in tropical islands of the Indo-Pacific region. The population of this species is declining in many island regions, mainly because of harvesting for human consumption, and because of habitat loss (Drew et al., 2010). Owing to the importance of their growth in resource management, several growth studies have focused on coconut crab (Fletcher et al., 1990; Drew et al., 2013; Sato et al., 2013; Oka et al., 2015). Although these studies analyzed the data obtained by mark and recapture methods, the modeled growth curves were either not obtained or the analysis was limited to a small number of samples. Our previous study (Oka et al., 2015) was the most accurate growth analysis; it examined 126 recapture cases, in an 8-year study period (2006–2014). The population size information is also important for conservation. Previous studies have estimated population density based on direct observation (Helfman, 1973; Schiller, 1992, 1998; Kadri-Jan, 1995; Chauvet & Kadiri-Jan, 1999; Buden, 2012; Drew & Hansson, 2014). However, no data are available on population size and density of coconut crabs in the Ryukyu archipelago, which is the northernmost area for the distribution of coconut crabs.

In this study, we conducted growth analysis and population estimation of coconut crabs in the Ryukyu archipelago using the statistical software R (R3.6.1; R Core Team, 2019). The data new recaptures from an additional survey conducted from 2015–2019, was used in addition to the data from our previous study (Oka et al., 2015).

A field investigation was conducted at Ocean
Expo Park (26°41’N and 127 52’E, 0.77 km²), which is managed by the Japanese government on Okinawa Island, southeast Japan. Coconut crabs are mainly observed close to coastal forests, depending on the location of prey and nest sites (Oka et al., 2014; Oka et al., 2016). A total of 1080 crabs were captured manually from 359 night surveys conducted during 2006–2019. The thoracic length (ThL; see Fletcher et al., 1990) of the captured crabs, was measured to the nearest 0.1 mm using vernier calipers, and the sex and capture point of each individual was recorded. Photographic matching of the grooving pattern on carapaces is a useful technique for long-term individual identification (Oka et al., 2013). A total of 1080 crabs were captured, and 189 individuals were recaptured, including a maximum of seven recapture cases. Data from 2006 to 2014 (485 crabs and 89 recaptures) were obtained from the raw data of the previous study (Oka et al., 2015).

Growth was estimated by analyzing the data obtained from the mark-recapture data. The input data comprised individual size increments, i.e., two sets of paired variables: time lags (dt) and size differences (dL), for each recapture event. The total number of datasets used were 506 (204 females, 302 males), and all recapture cases were combined. The dataset of both sexes was inserted into the grotagplus function of the fishmethods R package (Nelson, 2018) to calculate GROTAG, which is a growth estimation method based on the mark-recapture data and the parameters proposed by Francis (1988). The growth and von Bertalanffy growth function (VBGF) parameters generated by the grotagplus function are listed in Table 1. In this method, the data were fitted using a constrained maximum likelihood optimization (Nelson, 2018). Unlike the previous studies (Sato et al., 2013; Oka et al., 2015), evaluation of the optimal model from four model scenarios using the calculated likelihood value and Akaike’s information criteria (Francis, 1988) was not required in the first step of GROTAG analysis. The individual growth increments and the growth parameters K (growth coefficient) and Lmax (mean asymptotic length) of each sex obtained using grotagplus calculation were then used as inputs to plot increments on VBGF curves using the growthTraject function within the fishmethods package (Nelson, 2018).

Table 1. Growth and von Bertalanffy growth function (VBGF) parameters estimated based on mark-recapture data using the grotagplus function of the fishmethods R package. Estimated parameters were abbreviated as follows: ga, gb: mean annual growth at reference lengths α and β; m, s: mean and s.d. of the measurement error for length increment; nu: growth variability; p: outlier probability; Lmax: mean asymptotic length, K: growth coefficient

|              | Male (n = 302, α = 18, β = 68) | Female (n = 204, α = 21, β = 47) |
|--------------|-------------------------------|----------------------------------|
| gα           | 3.71 ± 0.22                   | 1.32 ± 0.13                      |
| gβ           | 0.23 ± 0.11                   | 0.13 ± 0.10                      |
| m            | 0.00 ± 0.13                   | 0.00 ± 0.09                      |
| s            | 0.92 ± 0.13                   | 0.45 ± 0.11                      |
| nu           | 0.45 ± 0.04                   | 0.68 ± 0.07                      |
| p            | 0.04 ± 0.02                   | 0.08 ± 0.03                      |
| Lmax         | 71.38                         | 50.79                            |
| K            | 0.072                         | 0.047                            |
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2018 showed a growth curve fitted with increments in measurement that was not drawn in previous studies (Fig. 1). The increment range shown in Fig. 1 can be regarded as the approximate range of growth. Drew et al. (2013) reported that a mark and recapture survey on Christmas Island found negative growth of coconut crabs that were injured by interspecific struggles. In the present study, 12 males and 5 females showed negative growth (Fig. 1). However, there was no record of whether the individuals who showed negative growth were injured. In addition, negative growth tended to be more in large males (> 55 mm TL) (Fig. 1). Drew et al. (2013) suggested that sexual differences in the frequency of injured coconut crabs was probably because males fight more aggressively than females, to defend food and other resources. Furthermore, male coconut crabs of large sizes have been shown to be more successful in breeding (Sato & Yoseda, 2010), and physical fighting depending on body size may likely occur while competing for mates.

We estimated the population size using the same package program and attempted to evaluate the state of the population. To the best of our knowledge, the present study is the first to use the mark-recapture dataset for population size estimation of coconut crab. The fishmethods package has also implemented the population size estimation program, called the Schnabel method (Krebs, 1999), which is based on repeated mark-recapture data. The Schnabel method can estimate the population size from more than two mark-recapture encounter datasets, and there is no limit on the maximum number of recaptures required (Krebs, 1999). The dataset consisting of the number of total captures, recaptures, and new captures of coconut crabs in each of the total 357 surveys were inserted into the schnabel function of the fishmethods package (Nelson, 2018). The results revealed that population size of coconut crabs in this area was 1045 individuals (95% CI: 955–1153). The forest area inhabited by coconut crabs was 11.2 ha in the Ocean Expo Park (Oka, 2017); therefore, population density was calculated to be 93.3/ha. The Ocean Expo Park is semi-enclosed, the capture of animals is prohibited, and natural coastal forests have been developed in its northern limit, where artificial stress is kept at minimum (Oka et al., 2014). To evaluate the significance of the population size obtained in this study, the population density obtained was compared with the population density data from previous studies in the tropical areas of the Indo-Pacific (Table 2). The previous studies were performed to estimate densities using direct observations. The results of the direct observation methods varied considerably depending on the season and area in Christmas Island (Drew & Hansson, 2014). Conversely, the estimation by Schnabel method (which relies on mark-recapture data), was not affected by such short-term variations, and provided a more accurate view of the population. Thus, the comparison of population densities in Table 2 was focused on discussing the overall trend, assuming the possibility of inaccuracy due to differences in estimation methods. The population density in the areas with harvest restrictions were clearly

Fig. 1. VBGF curve with “best fit” parameters obtained by mark-recapture datasets (male: bold solid line, female: dashed line). Thin lines derived from VBGF curves are actual increments fitted by the growthTraject function of the fishmethod R package. Solid thin lines indicate the increments that had negative growth at recapture intervals over one year.
higher than that in areas without restrictions. Although the density of coconut crabs in Ocean Expo Park was lower than that of the low latitude area where capture was restricted, it was denser than the population at Christmas Island (which is famous for having a large population of coconut crabs) (Table 2). Therefore, it can be concluded that the population density of the Ocean Expo Park is not low, even if we consider the environmental disadvantages of the northernmost area. The reproductive season and active season are shortest in the northernmost population compared to other populations (Oka et al., 2014).

The findings of growth and population size of the non-harvested population in the northern limit of this study will be useful for conservation of this endangered species in the Ryukyu archipelago. In the resource evaluation of the Ryukyu archipelago population based on size composition, sex ratio, and genetic analysis, the population outside Okinawa Island was found to be negatively affected by overfishing (Yorisue et al., 2020). In particular, the influence of selective harvesting of large males is an important factor affecting the reproduction of coconut crabs (Yorisue et al., 2020). The findings of the present study would be useful for resource management, such as setting harvest sizes and periods, for sustainable usage. The growth curves depicted in this study, will help to estimate the conservation period required to bring the decreasing population to a sustainable level, and the density information will serve as a reference value for optimal population density in the Ryukyu archipelago.

The R scripts and datasets used in this study are provided in the supplemental material. The format of the datasets should follow the manual of the fishmethods package (Nelson, 2018).

[Table 2. Comparative data on the density of the coconut crab at various locations]

| Location                     | Latitude     | Density (ind/ha) | Exploited population | Methods          | Source                        |
|------------------------------|--------------|------------------|-----------------------|------------------|-------------------------------|
| Ocean Expo Park, Okinawa     | 26°41’N      | 93.3             | No                    | Mark-recapture   | Present study                 |
| (Japan)                      |              |                  |                       |                  |                               |
| Taiaro (French Polynesia)    | 15°45’N      | 190.0            | No                    | Direct observation| Chauvet & Kadiri-Jan (1999)   |
| Enewetok Atoll (Marshall     | 11°21’N      | 147.0            | No                    | Direct observation| Helfman (1973)                |
| Islands)                     | 8°08’S       | 154–427          | Limited               | Direct observation| Buden (2012)                  |
| Christmas Island (Australia) | 10°30’S      | 16.3–47.3        | Limited               | Direct observation| Drew & Hansson (2014)         |
| Niue                         | 19°00’S      | 46.0             | Yes                   | Direct observation| Schiller (1992, 1998)         |
| Lifou Island (New Caledonia) | 21°00’S      | 27.5             | Yes                   | Direct observation| Kadiri-Jan (1995)             |

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[■ Literature Cited]

Buden, D. W., 2012. Coconut crabs, Birgus latro (Anomura: Coenobitidae), of Sorol Atoll, yap, with remarks on the status of B. latro in the Federated States of Micronesia. Pacific Science 66: 509–522.

Chauvet, C., & Kadiri-Jan, T., 1999. Assessment of an unexploited population of coconut crabs, Birgus latro (Linne, 1767) on Taiaro atoll (Tuamotu archipelago, French Polynesia). Coral Reefs, 18: 297–299.

Drew, M., Smith, M., & Hansson, B., 2013. Factors influencing growth of giant terrestrial robber crab Birgus latro (Anomura: Coenobitidae) on Christmas Island. Aquatic Biology, 19: 129–141.

Drew, M. M., & Hansson, B. S., 2014. The popu-
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- **Francis, R. I. C. C., 1988.** Maximum likelihood estimation of growth and growth variability from tagging data. New Zealand Journal of Marine and Freshwater Research, 22: 43–51.

- **R Core Team, 2019.** R: A language and environment for statistical computing. https://www.R-project.org/. R Foundation for Statistical Computing Vienna, Austria.

- **Schiller, C. B., 1992.** Assessment of the status of the coconut crab *Birgus latro* on Niue Island with recommendations regarding an appropriate resource management strategy. Consultancy report prepared for the Food and Agricultural Organization of the United Nations. University of Queensland Queensland, Australia.

- **Schiller, C. B., 1998.** Pilot stock survey of the coconut crab (*Birgus latro*) in Niue Islands, Pacific Ocean. Consultancy report. FAO: Rome Italy.

- **Yorisue, T., Iguchi, A., Yasuda, N., Yoshioka, Y., Sato, T., & Fujita, Y., 2020.** Evaluating the effect of overharvesting on genetic diversity and genetic population structure of the coconut crab. Scientific Report: 10026.
Addresses
(SO) (KT) Okinawa Churashima Foundation, 888 Ishikawa, Motobu, Okinawa 905–0206, Japan
(TI) National Institute for Materials Science, 1–2–1 Sengen, Tsukuba 305–0047, Japan

E-mail address of corresponding author
(SO) sh-oka@okichura.jp