

Expansion of the Northern Geographical Distribution of Land Hermit Crab Populations: Colonization and Overwintering Success of *Coenobita purpureus* on the Coast of Boso Peninsula, Japan

Tetsuya Sanda^{1,2}, Katsuyuki Hamasaki^{1,*}, Shigeki Dan¹, and Shuichi Kitada¹

¹Department of Marine Biosciences, Tokyo University of Marine Science and Technology, Konan, Minato, Tokyo 108-8477, Japan. *Correspondence: E-mail:

hamak@kaiyodai.ac.jp (Hamasaki) E-mail: sdan@kaiyodai.ac.jp (Dan);

kitada@kaiyodai.ac.jp (Kitada)

²Present Address: Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute, Japan Fisheries Research and Education Agency, Fukai-Ota, Ishigaki, Okinawa 907-0451, Japan. E-mail: sanda@affrc.go.jp (Sanda)

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The present study aimed to elucidate the population dynamics of land hermit crabs on the coast of the Boso Peninsula, Chiba Prefecture, Japan, which is the northern limit of their geographical distributions. We conducted monthly field surveys at four sites from April 2012 to December 2014 and visually searched for crabs. Laboratory experiments were also conducted to evaluate the overwintering ability of the two species *Coenobita purpureus* and *C. rugosus* that were detected in the field surveys; adult crabs and laboratory-raised juveniles were exposed to low-temperature conditions that simulated the *in situ* temperatures during the early overwintering period. Newly landed juveniles first appeared in August. They were identified as either *C. purpureus* or *C. rugosus* and *C. purpureus* was the dominant species. Early juveniles grew until October. The abundance of early juveniles decreased in accordance with decreasing air temperatures, and dead individuals were found during the overwintering period. The low-temperature tolerance ability of *C. purpureus* was stronger than that of *C. rugosus*. Some crabs successfully overwintered, and all were identified as *C. purpureus*. The growth and overwintering success of juveniles varied among the survey sites depending on the local temperature regime. Our results highlighted the frontier for expanding the northern geographical distribution of land hermit crab populations by the colonization and overwintering success of *C. purpureus*.

Key words: Terrestrial hermit crabs, Biogeography, Larval dispersal, Thermal adaptation, Low-

temperature tolerance.

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BACKGROUND

Many benthic marine organisms can expand their geographical distributions through the pelagic larval stage (Cowen and Sponaugle 2009), and larval transport and dispersal largely depend on ocean circulation patterns (Williams and Hastings 2013). Poleward-flowing currents, *i.e.*, western boundary currents, such as the Kuroshio Current and the East Australian Current, transport larvae from warmer to cooler latitudes (Ling et al. 2009; Chang et al. 2018); therefore, the successful colonization of poleward habitats by species from warmer habitats should critically rely on the low-temperature tolerance abilities of the species.

Terrestrial hermit crabs of the family Coenobitidae Dana 1851 are mainly distributed in subtropical and tropical coastal regions (Hartnoll 1988). They comprise land hermit crabs of the genus *Coenobita* Latreille 1829, with approximately 17 species, as well as the coconut crab *Birgus latro* (Linnaeus 1767), which is the only species in the genus *Birgus* Leach 1816 (Hartnoll 1988; Poupin 1996; McLaughlin et al. 2010; Rahayu et al. 2016). After hatching on shores, coenobitid larvae spend their pelagic life through zoeal stages to megalopae for several weeks in the sea (Hamasaki et al. 2015a); then, after settlement, megalopae acquire empty gastropod shells and emigrate from the sea to land (Hamasaki et al. 2015b).

Coenobitid crabs are primarily subtropical and tropical species; however, *C. purpureus* Stimpson 1858 is endemic to the northwestern Pacific region (mainly > 24°N). Five other coenobitid species, which are widely distributed in the Indo-West Pacific region, *i.e.*, *B. latro*, *C. brevimanus* Dana 1852, *C. cavipes* Stimpson 1858, *C. rugosus* H. Milne-Edwards 1837, and *C. violascens* Heller 1862, also commonly occur on the southern islands of Japan (Kagoshima Prefectural Board of Education (KPBE) 1987; Okinawa Prefectural Board of Education (OPBE) 1987; Nakasone 1988, 2001; Fujikawa et al. 2017; Hamasaki et al. 2017a; Sanda et al. 2018a b). *C. purpureus* has the northern-most geographical distribution (35°N), followed by *C. rugosus* (31°N) on the Pacific coasts of Japan (Oyake and Fujikawa 2009; Miura 2011). Sanda et al. (2019) evaluated the low-thermal tolerance abilities of laboratory-raised juveniles with ~1 mm shield length (SL) of six coenobitid species that occur in Japan by estimating the median lethal temperature (MLT) at which 50% of the test juveniles had died. They found that the most northward

distributed species, *C. purpureus*, had the lowest MLT values, and the MLT estimates significantly decreased with increasing latitude toward the northern limit of the geographical distributions of the six coenobitid species.

Estuarine decapod crustaceans with meroplanktonic larvae generally exhibit two life history strategies during the larval phase (Strathmann 1982; Anger 2001): 1) retention strategy—larvae develop within estuaries with unstable and low salinity conditions and 2) export strategy—zoeae disperse through coastal or offshore areas with stable and high salinity conditions, and megalopae migrate to the estuarine habitat for initiating the benthic life. In species using the retention strategy, all larval stages are better adapted to low salinity conditions, whereas in species exhibiting the export strategy, the low salinity tolerance limit for survival is lowest in newly hatched larvae, that increases during the zoeal stage and declines in a megalopal stage (Costlow et al. 1966; Cronin 1982; Anger 1991; Charmantier et al. 2002; Anger et al. 2008). Hamasaki et al. (2018a) examined the low salinity tolerance ability of zoeal and megalopal larvae of the six coenobitid species that occur in Japan and found the similar larval traits in all species; early zoeae and megalopae were euryhaline and later zoeae stenohaline, suggesting that coenobitids exhibit a larval export strategy towards the offshore (oceanic) marine waters. The Kuroshio Current plays an important role for transferring larvae of southern marine organisms from warmer to cooler latitudes in the northwestern Pacific region (Veron and Minchin 1992; Iida et al. 2010; Soeparno et al. 2012; He et al. 2015; Yuhara et al. 2017; Chang et al. 2018). Thus, it can be considered that pelagic larvae of coenobitid crabs disperse broadly throughout the southern islands and Pacific coast of Japan via the Kuroshio Current and its countercurrents (Fig. 1); then, the megalopae migrate onto land there. This might be supported by the genetic panmixia of the *C. purpureus* populations that were collected from Ishigakijima Island, Okinawajima Island and Takarajima Island in the Ryukyu Archipelago through Otsuki on the Pacific coast of Japan to Hachijojima Island, which the Kuroshio Current flows directly to (Hamasaki et al. 2017a) (Fig. 1).

The reproductive season of coenobitid crabs occurs in summer in Japan (KPBE 1987; OPBE 1987; Nakasone 2001; Fujikawa et al. 2017). The differences in air temperature are small (< 3.5°C) in summer throughout the geographical distribution of coenobitids in Japan, whereas the winter temperatures decrease in accordance with northward latitudes, and their maximum difference is approximately 13°C (Sanda et al. 2019). Therefore, it can be hypothesized that after landing, early juveniles might die, depending on species-specific low-temperature tolerance properties during the overwintering period, leading to the current biogeographical pattern of coenobitid species. Ikeda and Imafuku (1987) found early juveniles of coenobitids on the coast of Shirahama, Wakayama Prefecture, Japan (Fig. 1) and detected dead juveniles during the overwintering period. Early juveniles were identified as *C. purpureus* and *C. rugosus* after being cultured for 1–2 years (Ikeda

and Imafuku 1987). *Coenobita rugosus* possibly died during the overwintering period because only subadult and adult *C. purpureus* were found on the coast of Shirahama (Imafuku and Ikeda 1987; Kubota 2011 2013). However, the species composition of the early juveniles was unknown, and little is currently known about the population dynamics of early coenobitid species after landing on the Pacific coast of Japan.

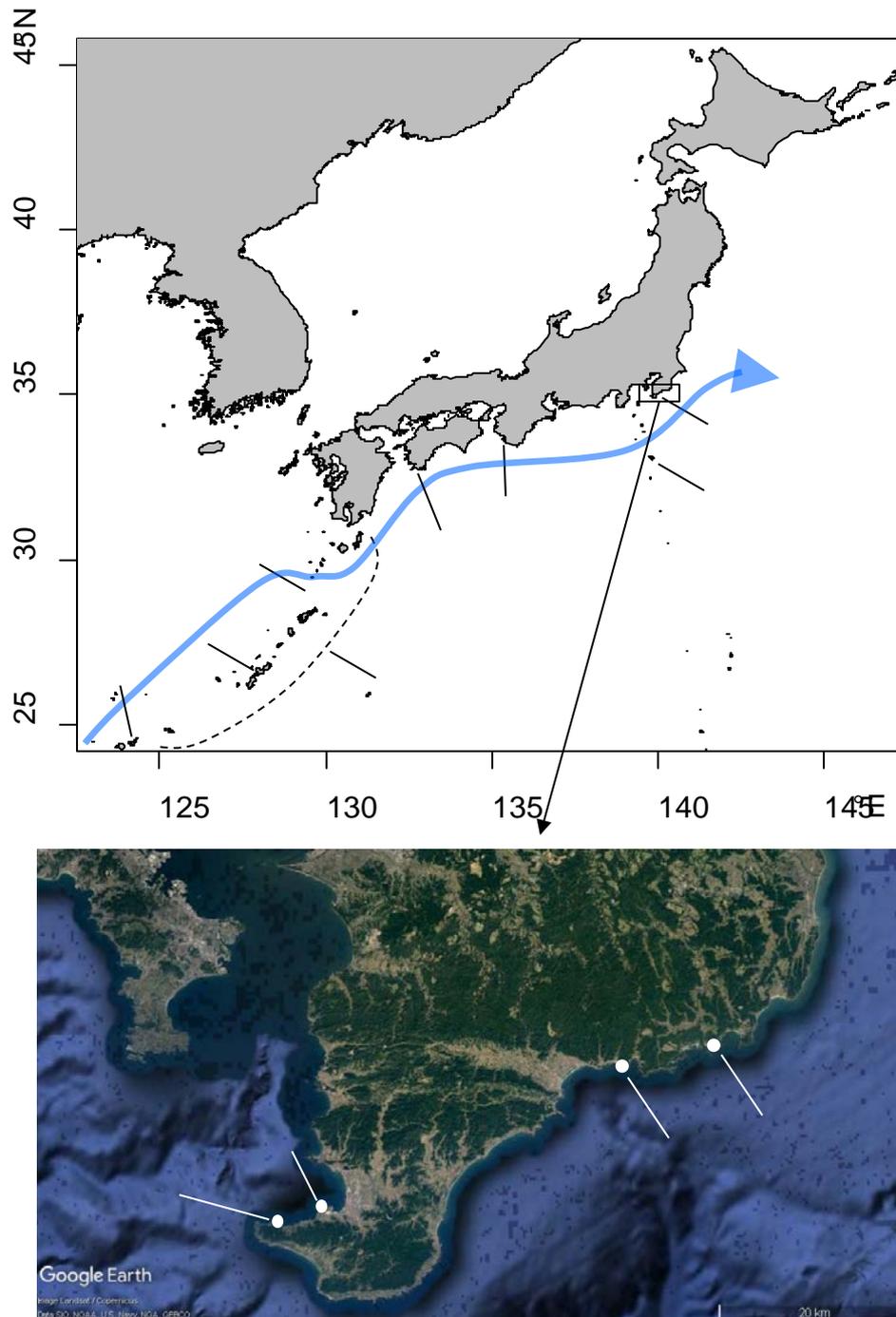


Fig. 1. Map showing the Ryukyu Archipelago and the Pacific coast of Japan with information on the Kuroshio Current (KC) in the northwestern Pacific region (a) and Google Earth photograph showing the southern Boso Peninsula, Japan (b). The blue line shows the KC. The dotted line indicates the Ryukyu

Archipelago (RK). Other locations referred to in the main document are as follows: IG, Ishigakijima Island; ON, Okinawajima Island; TA, Takarajima Island; HJ, Hachijojima Island; OT, Otsuki; SH, Shirahama; BP, Boso Peninsula (a); BN, Banda; OK, Okinoshima, NJ, Cape Nojimizaki; SR, Shirosaki; KT, Katsuura; TB, Tateyama Bay (b).

Our objective in the present study was to test this hypothesis by investigating the species composition and population dynamics of early juveniles after landing on the coast of the Boso Peninsula, Chiba Prefecture, Japan. We also evaluated the low-temperature tolerance traits of juvenile and adult coenobitids in species, *C. purpureus* and *C. rugosus*, which were detected on the Boso Peninsula, by laboratory experiments to elucidate the overwintering abilities of these species. Our surveys highlight the frontier for expanding the northern geographical distribution of land hermit crab populations by the colonization and overwintering success of *C. purpureus*.

MATERIALS AND METHODS

Field study

All species of land hermit crabs of the genus *Coenobita* in Japan are recognized collectively as natural monument animals. Therefore, field study was carried out under permission (License Certificate No. 4-1892) from the Chiba Prefectural Board of Education and the Agency for Cultural Affairs, Government of Japan.

The field study was conducted on the coast of the Boso Peninsula, Chiba Prefecture, Japan, from April 2012 to December 2014. The Boso Peninsula is located on the middle part of Japan (Fig. 1) and the northernmost region where marine biodiversity is directly influenced by the Kuroshio Current in the northwestern Pacific region (Hagiwara 2003; Yamano and Namizaki 2009; Yamano et al. 2011; Sunobe et al. 2014). Two sites, Banda (34°58'N, 139°46'E) and Okinoshima (34°59'N, 139°49'E), on the coast of the inner Boso Peninsula in Tateyama Bay, and two sites, Shirosaki (35°7'N, 140°10'E) and Katsuura (35°8'N, 140°17'E), on the coast of the outer Boso Peninsula facing the Pacific (Fig. 1), were chosen for the field survey based on preliminary information from colleagues that coenobitid juveniles were found there. Survey sites were natural sandy/cobble beaches with rocky areas, and the supratidal zones at Banda, Okinoshima and Katsuura were generally vegetated with grasses and shrubs that intermingled with coastal forests, but Shirosaki had no coastal forests because its supratidal zone was connected with artificial embankments and facilities. Photographs of survey sites are shown in figure S1.

Monthly surveys were conducted from April 2012 at Banda, September 2012 at Okinoshima, August 2012 at Shirosaki, and February 2013 at Katsuura. We visited each site once late in each month, and 1 or 2 persons visually surveyed coenobitid crabs for 1 h or 0.5 h in the afternoon. Crabs were mainly found near or under cobbles or rocks. We collected crabs by hand and temporarily kept them in containers. Crabs that were not able to be captured were visually counted on-site. We measured the SL or dactylus length (DL) of the left third pereopod (in mm) of the captured crabs on-site according to Fujikawa et al. (2017) and Hamasaki et al. (2017b). Measurements were conducted using Vernier calipers with the aid of a magnifying glass ($\times 3.5$). DL was converted to SL according to Fujikawa et al. (2017) for larger crabs (> 2.5 mm SL; $SL = 1.163 \times DL$) and using a regression equation established for smaller crabs (< 2.5 mm SL; $SL = 0.9493 \times DL + 0.2519$) using specimens in the present study and those collected on Hachijojima Island and Takarajima in our previous field studies (Sanda et al. 2018a, b) (see Fig. S2). Collected crabs were released on-site after body size measurements.

The diagnostic features identifying the six coenobitid species that occur in Japan are their distinct body color patterns as juveniles with > 1.5 mm SL (Hamasaki et al. 2017b) and the outer left chela morphology of juveniles with > 2 mm SL (K. Hamasaki, unpublished data). Therefore, the species of collected crabs with > 2 mm SL were morphologically identified in accordance with Nakasone (1988), Asakura (2004), and Hamasaki et al. (2017b). In our field surveys, we were legally permitted to collect 30, 50 and 60 juveniles for specimens in 2012, 2013 and 2014, respectively. Newly landed juveniles began to appear in August on the Boso Peninsula (see the Results section). Therefore, to elucidate the species of early juveniles just after landing on the Boso Peninsula, early juveniles with approximately 1 mm SL were collected and preserved in 99.5% ethanol in August or September for genetic identification of the species according to the method of Hamasaki et al. (2018b). The number of specimens collected from each site is summarized in Table S1. Genomic DNA was extracted from the whole body of each specimen and the internal transcribed spacer region was amplified with a polymerase chain reaction (PCR) technique. Then, we identified the species-specific banding patterns in restriction fragment length polymorphism of the PCR amplification products which are generated with a restriction endonuclease *MspI* (Takara Bio, Kusatsu, Shiga, Japan) and visualized on a 1.5% agarose gel.

In the present study, the overwintering period of coenobitid crabs was defined as the period from November to April when the mean air temperature was generally below 18°C because many coenobitid juveniles cease feeding below $\sim 18^{\circ}\text{C}$ (Sanda et al. 2019). To infer the temperature environments of the early juvenile habitats during the overwintering period, the air temperature was recorded every 15 min with a data logger (Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan) at three sites (except for Katsuura) from December 1, 2013 to March 11, 2014, and at all

sites from November 1 to December 22, 2014. A data logger was also placed under the cobbles or rocks where many juveniles were found.

Low-temperature tolerance experiment

Sanda et al. (2019) evaluated the low-temperature tolerance abilities of *C. purpureus* and *C. rugosus* by exposing laboratory-raised juveniles (approximately 1 mm SL) to the decreasing temperature conditions from 27°C (1°C reduction every two days) over a period of approximately three weeks. To further elucidate the low-temperature tolerance abilities of these two species, we conducted two laboratory experiments in 2014 by exposing adult crabs to constant low-temperature conditions (experiment 1) or adult and juvenile crabs to the cyclic low-temperature conditions that simulated the field temperature fluctuation regime during the early winter (experiment 2) in a temperature-controlled incubator chamber and determining their survival. Adult crabs with approximately 7 mm SL were purchased from a commercial pet trader, and juveniles with approximately 1 mm SL were prepared by culturing larvae hatched from females collected on Ishigakijima Island according to the method of Sanda et al. (2019) (Tables S2 and S3). We got permission (License Certificate No. 4-2058) from the Okinawa Prefectural Board of Education and the Agency for Cultural Affairs, Government of Japan to collect ovigerous females of *C. purpureus* and *C. rugosus*. Test crabs were individually housed in small plastic cups (adult, 101 mm diameter, 80 mm height, 465 mL volume; juvenile, 87 mm diameter, 42 mm height, 120 mL volume) covered with a top with two small air vents (~1.5 mm diameter). Coral sand was spread on the bottom of the cups at a depth of ~30 mm (adult) or 10 mm (juvenile), and small coral fragments were provided on the sand as shelters for the crabs. To maintain the moist condition in the culture cup, the sandy bottom surface was misted with freshwater at the beginning of the experiment. Crabs were not fed during the experiment.

Experiment 1 was conducted from late August to early September, and five constant temperature levels, 2, 4, 6, 8 and 10°C, were tested. Crabs were set in the same incubator chamber controlled at ~25°C with a photoperiod of 12 h light:12 h dark (MT1–201, Tokyo Rikakikai Co. Ltd., Tokyo, Japan). Then, crabs were acclimated for 24 h at ~15°C, kept for 12 h at the test temperature level, and recovered after 12 h at ~25°C. The death of the crabs was confirmed by their lack of reaction to physical stimulation with forceps. Two trials were carried out using 13 or 12 individuals per trial (total 25 crabs) for both species at each test temperature level, except for 2°C, in which one trial was conducted using 25 individuals of *C. purpureus*. *C. rugosus* was not tested at 2°C because all *C. rugosus* had died at the 4°C test level. One incubator was available in the laboratory so that the test trial was conducted every two days from 10°C to 2°C levels. The air

temperature was recorded every 15 min using a data logger set in a test cup without a crab in the incubatory chamber. The temperature profile is shown for each test trial in Fig. S3, and the mean temperature values are summarized for each test trial during the acclimation, testing and recovery periods in Table S4.

Experiment 2 was conducted from late October to November. The temperature fluctuation regime, a 24 h cycle fluctuation between $\sim 8^{\circ}\text{C}$ and 15°C , was recorded at Okinoshima during the early winter (10–16 December 2013) (see Fig. S4a) when dead juveniles were found, was simulated in the test incubator. Two trials were conducted using a total of 25 adult crabs of both species as performed in experiment 1, and the mortality of each crab was determined every 24 h until all of the crabs had died (trial 1, 6 days; trial 2, 8 days). For juveniles of both species, one trial was conducted using 25 individuals, and observations of juveniles were repeated for nine days. The air temperature was recorded every 15 min and is shown for each trial in Fig. S4b–d. The 24 h temperature fluctuation cycle could be simulated in the trial using juveniles (nine cycles for nine days), but the temperature fluctuation cycle was somewhat shorter than 24 h in the trials using adult crabs probably because of a time-lag in the time controller (eight cycles for six days in trial 1 and ten cycles for eight days in trial 2).

Data analysis

The size-frequency distributions with 0.2 mm SL intervals were summarized monthly for each survey site to distinguish between the early juveniles in an age-0 group and larger crabs in an age-1 < group (Fig. S5A–C). Newly landed juveniles were found starting in August on the Boso Peninsula. Overall, newly landed juveniles were in the 0.8–1 mm SL class and grew until October. Generally, this cohort had a unimodal size frequency distribution, and the largest juveniles of the cohort were in the 2.4–2.6 mm SL class until the next June or July (Fig. S5A–C). The overwintering crabs from the 2.4–2.6 mm SL class were also found in August when the new recruitment occurred (Fig. S5B, C). Thus, we considered a 2.8 mm SL as a boundary size distinguishing the age-0 and age-1 < group.

Statistical analyses were performed using R statistical software (R3.5.2; R Core Team 2018) at the 5% significance level. We used a generalized linear model (GLM) or a linear model (LM) (Zuur et al. 2009). A quasi-Poisson GLM was used to account for overdispersion of the count data when comparing the abundance of newly landed juveniles (age-0) among the survey sites and years. LM analysis was performed to compare the abundance of overwintered juveniles (age-1 <) after the number of juveniles (n) was logarithmically transferred as $\log_e(n + 0.5)$ (Yamamura 1999) because all count data were zeros at Banda. LM analysis was also performed to compare the growth of early

juveniles (age-0). In these analyses, survey sites and years were the categorical explanatory variables, and the response variables were as follows: the abundance of newly landed juveniles as the maximum number of age-0 juveniles counted on each site until October before the beginning of the overwintering period in respective years; the abundance of overwintered age-1 juveniles as the cumulative total number of age-1 < crabs counted on each site from August 2012 to July 2013, August 2013 to July 2014, and August 2014 to December 2014; and growth as the shield length of individuals in October in respective years because age-0 juveniles grew from August until October (see the Results section). The daily mean air temperature during the overwintering period (response variable) was also compared among the survey sites (categorical explanatory variable) by an LM analysis. The GLM and LM analyses were performed with *glm* function and *lm* function, respectively. The statistical significance of the explanatory variable was evaluated with an *F*-test using the *Anova* function (Type II) (Fox and Weisberg 2011). Two species, *C. purpureus* and *C. rugosus*, were identified in newly landed juveniles (see the Results section). Because of the small sample sizes at each site for species identifications (Table S1), we pooled the data from all of the sites in each year and used them to test the null hypothesis (true probability of each species is equal to 0.5) by an exact binomial test using the *binom.test* function.

In laboratory experiment 1, using the results from both trials, the relationship between the mean test temperature (x) and survival rate of crabs (y) was formulated by a logistic equation: $y = 1/(1+e^{-(a+bx)})$, where a and b are parameters. The parameters were estimated using a quasi-binomial GLM (logit link), and the MLT with a 95% confidence interval was estimated as the temperature at which 50% of the test juveniles had died using the *invest* function (Greenwell and Schubert Kabban 2016). In laboratory experiment 2, to compare the crab survival among the species, a log-rank test was performed with the *survdiff* function (Therneau 2018).

RESULTS

Field study

Newly landed juveniles could be genetically identified as either *C. purpureus* or *C. rugosus* except for one specimen in 2013 of which DNA could not be amplified. The species composition varied among the survey years (Fig. 2, Table S1), but *C. purpureus* was the dominant species, accounting for 80.0% ($P = 0.0014$), 73.5% ($P = 0.0014$), and 65.0% ($P = 0.0273$) of the crab samples in 2012, 2013, and 2014, respectively. Larger crabs with > 2 mm SL were all morphologically identified as *C. purpureus*.

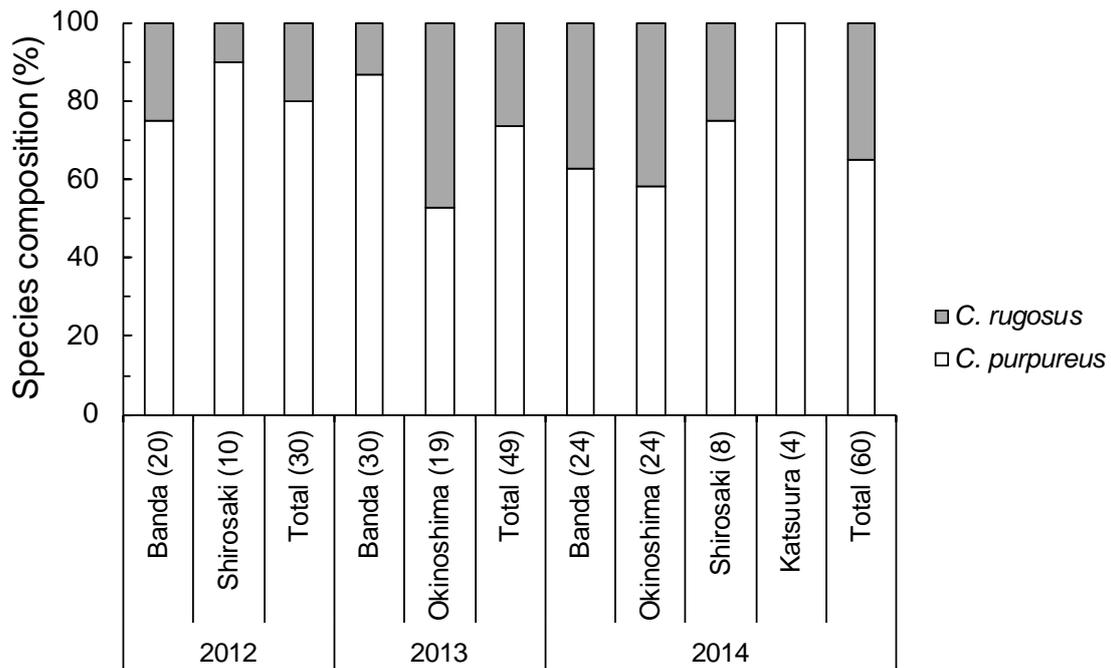


Fig. 2. Species composition of newly landed juveniles of coenobitid crabs at four sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan in 2012–2014. The number of specimens is shown in parentheses.

The number of individuals counted for age-0, age-1<, and the number of dead crabs are shown for each survey site in figure 3 (see raw data in Table S5). The newly landed juveniles were first found in August and after that, they increased in number; then, age-0 juveniles declined in accordance with decreasing air temperature. Some dead age-0 juveniles were found during the overwintering periods. Overall, the newly landed juveniles were abundant in 2012 at Banda and Okinoshima; the abundance of new recruits significantly varied among the survey sites ($df = 3$, $F = 13.60$, $P = 0.0077$) and years ($df = 2$, $F = 21.62$, $P = 0.0035$). Age-1< crabs were not observed at Banda and were abundant at Shirosaki; the total number of age-1< crabs counted significantly varied among the survey sites ($df = 3$, $F = 5.677$, $P = 0.0457$) but not among the years ($df = 2$, $F = 0.0807$, $P = 0.9237$).

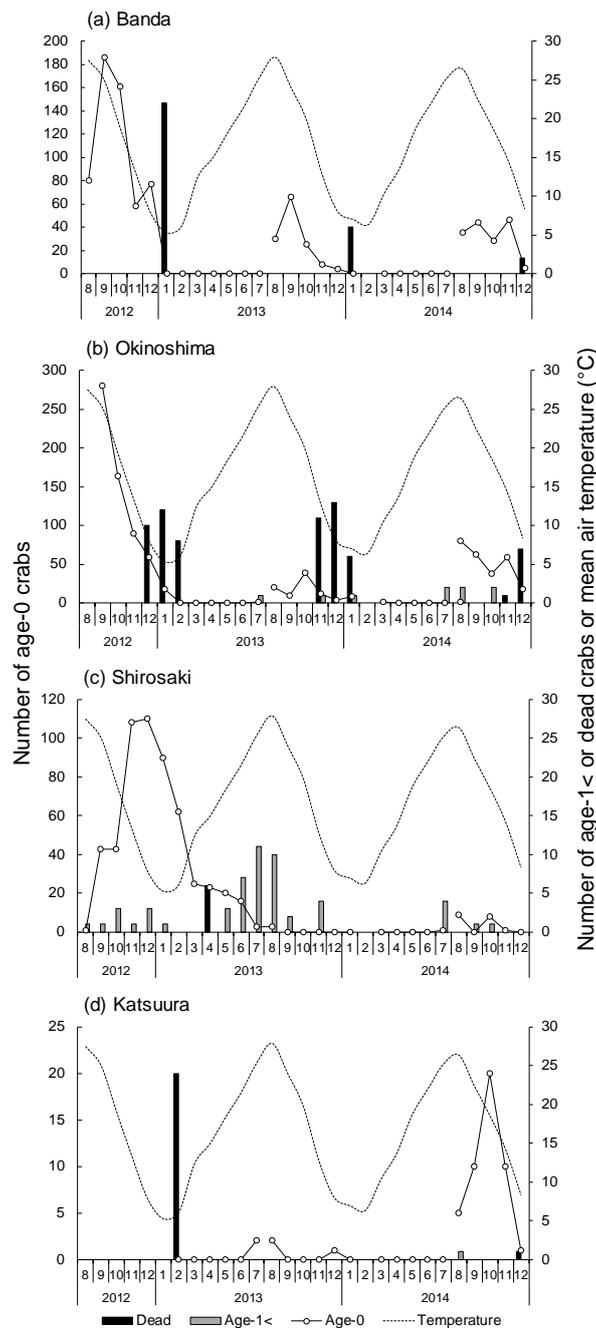


Fig. 3. Numbers of age-0, age-1< and dead coenobitid crabs counted at four survey sites (Banda (a), Okinoshima (b), Shirosaki (c), and Katsuura (d)) on the coast of the Boso Peninsula, Japan in 2012–2014. Age-0 crab, <2.8 mm SL; Age-1< crab, \geq 2.8 mm SL. Monthly mean air temperatures measured at the meteorological station (34°59.2'N, 139°51.9'E) (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>) in Tateyama City including Banda and Okinoshima are shown in each panel. The temperature profile in Tateyama City is similar to that in Kamogawa City (Shirosaki) and Katsuura City (Katsuura).

The changes in the mean SL of age-0 juveniles are illustrated in figure 4 (see sample number, and the mean and standard deviations in Table S6). The mean SL of the newly landed juveniles was approximately 0.9 mm. The juveniles grew linearly until October, and their growth tended to cease

during the overwintering period at each site except for Shirosaki where juveniles appeared to grow from February to March. A significant difference was detected in early juvenile body sizes before the overwintering period (October) among the survey sites ($df = 3, F = 10.59, P < 0.0001$) but not among the years ($df = 2, F = 1.662, P = 0.1920$). The body size of age-0 juveniles tended to be large at Shirosaki, followed by Okinoshima and Katsuura, and small at Banda. Age-1< crabs had a broad range of body sizes from 3–8 mm SL (Fig. S5A–C); the growth trend was not traced in age-1< crabs because of a small sample size. Ovigerous females were not found in the surveys.

Mean air temperatures at survey sites generally decreased below 20°C from November (Fig. S6, Table S7). The air temperatures significantly varied among the sites in both the 2012 ($df = 2, F = 24.38, P < 0.0001$) and 2013 surveys ($df = 3, F = 7.746, P < 0.0001$), and they tended to be high at Shirosaki, followed by Okinoshima and Katsuura, and low at Banda.

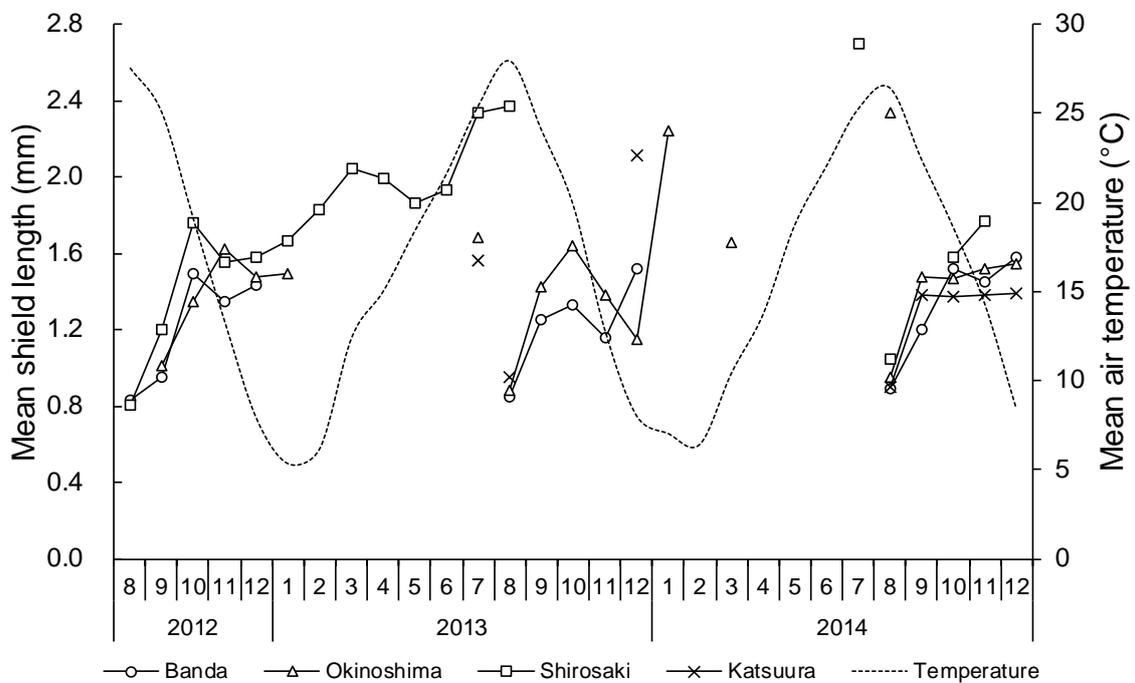


Fig. 4. Mean shield length of age-0 juveniles of coenobitid crabs at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan in 2012–2014. See Fig. 3 for the monthly mean air temperatures.

Low-temperature tolerance experiment

In experiment 1 under constant low-temperature conditions, adult crabs of *C. purpureus* exhibited higher low-temperature tolerances than those of *C. rugosus* (Fig. 5). Logistic equations were fitted to the relationship between mean test temperatures and the survival rates in each species

(Table S8), and the MLT with a 95% confidence interval was estimated at 4.69°C (4.35–5.04°C) for *C. purpureus* and 6.35°C (5.41–7.36°C) for *C. rugosus*.

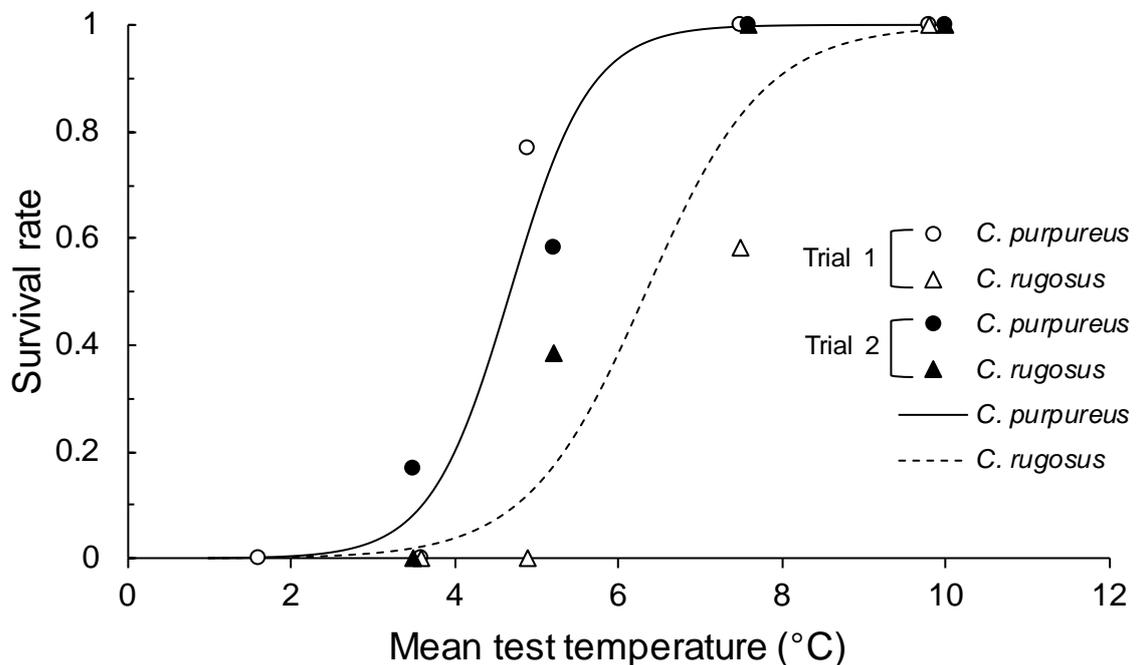


Fig. 5. Survival rate of adult crabs of *Coenobita purpureus* and *C. rugosus* in experiment 1 to evaluate low-temperature tolerance abilities under constant low-temperature conditions. Curves were calculated from the logistic equations estimated using the data of two trials for the respective species (see Table S8).

In experiment 2 under the simulated cyclic low-temperature conditions following those of the *in situ* environment, adult crabs of *C. purpureus* survived longer than those of *C. rugosus* in both trials (Fig. 6a), and significant differences were detected in survival between the two species (trial 1, $df = 1$, $\chi^2 = 4.502$, $P = 0.0339$; trial 2, $df = 1$, $\chi^2 = 18.30$, $P < 0.0001$). The difference in survival of juveniles was distinct between species ($df = 1$, $\chi^2 = 55.06$, $P < 0.0001$); only one *C. purpureus* juvenile died during the experiment period of nine days, but all *C. rugosus* juveniles had died by the eighth day (Fig. 6b).

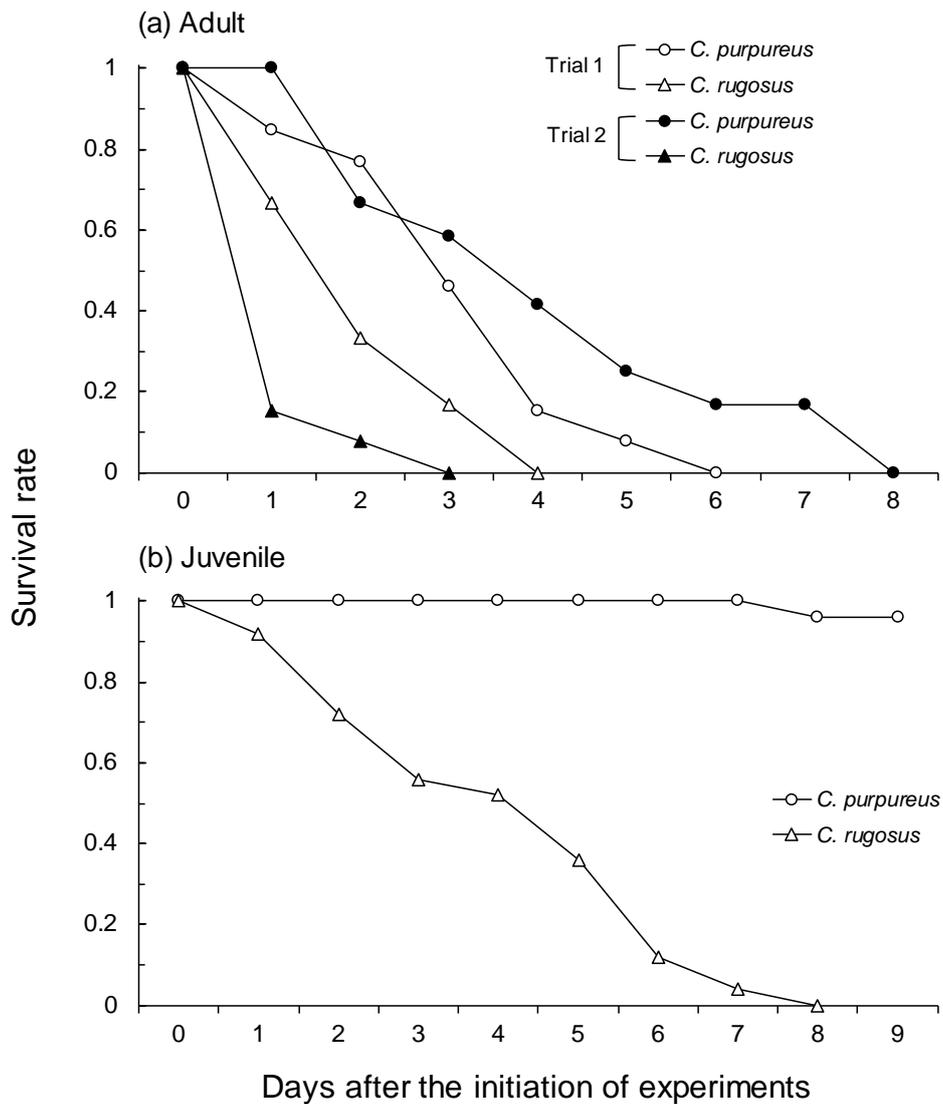


Fig. 6. Survival rates of adult (a) and juvenile (b) crabs of *Coenobite purpureus* and *C. rugosus* in experiment 2 to evaluate low-temperature tolerance abilities under the cyclic low-temperature conditions that simulated *in situ* daily temperature fluctuation.

DISCUSSION

Recruitment of land hermit crabs

Our field surveys revealed that newly landed, juvenile coenobitid crabs appeared in August on the Boso Peninsula, Japan; they were comprised of two species, *C. purpureus* and *C. rugosus*, and *C. purpureus* was the dominant species accounting for 65–80% of the new recruits (Fig. 2). The body sizes of the newly landed juveniles were approximately 0.9 mm SL (Fig. 4), which is equivalent to the body size of the first crab stage of these species raised in the laboratory (Hamasaki

et al. 2017b). Coenobitid megalopae migrate from the sea to the land after acquiring gastropod shells and bury themselves in sand before metamorphosis; then, they emerge as the first crab stage (Hamasaki et al. 2015b). Therefore, early juveniles found in August should be the first crab stage to emerge from burrows in the substratum on shores. Larvae of *C. purpureus* and *C. rugosus* require approximately 30–40 days before migrating onto shores as megalopae carrying gastropod shells (Hamasaki et al. 2015a, b), and the megalopae metamorphose into the first crab stage 5–6 days after landing at ~28°C (Hamasaki et al. 2015b), which is equivalent to the environmental temperatures during the reproductive season in summer. Therefore, newly landed juveniles that were found in late August in our surveys might have hatched from early to middle July. It has been reported that the larval hatching seasons of *C. purpureus* and *C. rugosus* occur from middle/late June to late September and from late June to late November, respectively, in the Ryukyu Archipelago (Imafuku 2001; Nakasone 2001).

Overwintering success of land hermit crabs

Fujikawa et al. (2017) collected *C. rugosus* through visual surveys during daytime and nighttime from late June to early July along the coast of Ishigakijima Island (Fig. 1). They showed that smaller (mode of 3–6 mm SL class) and larger crabs (mode of 6–9 mm SL class) tended to be captured during daytime and nighttime surveys, respectively, because of nocturnal behavior of larger crabs, and the number of crabs collected was larger during nighttime than daytime surveys. Due to the difficulty of searching for small juveniles of coenobitid crabs during the nighttime, Hamasaki et al. (2018b) visually sought and collected early juveniles (< 2 mm SL) during the afternoon and morning surveys. Our field surveys conducted in the afternoon might have underestimated the abundance of the crabs, particularly larger crabs. Nevertheless, our results could be spatially and temporally comparable because we adapted the same survey methodology during the field study.

The number of early juveniles largely decreased in accordance with decreasing air temperatures, and dead juveniles were found during the overwintering period from November to April (Fig. 3). All larger juveniles with >2 mm SL in age-0 and age-1 < groups were morphologically identified as *C. purpureus*. Sanda et al. (2019) demonstrated that juveniles of *C. purpureus* had the lowest MLT value among those of six coenobitid species that occur in Japan. In the present study, laboratory experiments also showed that adult *C. purpureus* exhibited a stronger low-temperature tolerance ability than adult *C. rugosus* (Fig. 5), and all *C. rugosus* juveniles died, but almost all *C. purpureus* survived under the temperature regime that simulated the *in situ* daily temperature fluctuations during the early overwintering period in middle December (Fig. 6).

Therefore, even though *C. rugosus* megalopae successfully landed and metamorphosed into the first crab stage on the Boso Peninsula (34°58'–35°08'N, 139°46'–140°17' E), all died depending on their low-temperature tolerances during the overwintering period. On the other hand, *C. purpureus* successfully colonized and overwintered on the Boso Peninsula. Sanda et al. (2018a) also inferred unsuccessful overwintering in the juveniles of *C. rugosus* on Hachijojima Island (33°02'–09'N, 139°44'–51'E) (Fig. 1) because they detected early juveniles of *C. purpureus* and *C. rugosus* based on the genetic identification method, but no adult *C. rugosus* individuals. *C. purpureus* and *C. rugosus* colonized the coast of Shirahama (33°40'–42'N, 135°19'–21'E) (Fig. 1), but only the *C. purpureus* population became established, and the females reproduced there (Ikeda and Imafuku, 1987; Imafuku and Ikeda 1987; Kubota 2011, 2013). Ovigerous females were not found on the Boso Peninsula, even though some crabs reached the maturity size for *C. purpureus* females (4 mm SL) (Nakasone 2001). Temperature is an important environmental factor affecting reproduction of decapod crustaceans; higher temperatures induce ovarian maturation or spawning (Matsuda et al. 2002; Hamasaki et al. 2004; Bembe et al. 2017). Air temperatures are generally higher at Shirahama than Tateyama (Fig. S7), and this might affect the reproduction of *C. purpureus* populations.

Newly landed juveniles grew linearly until October before the beginning of the overwintering period (Fig. 4). The body sizes of the early juveniles were different among the sites, and tended to be large at Shirosaki, followed by Okinoshima and Katsuura, and small at Banda. Age-1 < crabs were also abundant at Shirosaki and were found at Okinoshima and Katsuura, but not at Banda. The air temperature measured at each site during the early overwintering period tended to be high at Shirosaki, followed by Okinoshima and Katsuura, and low at Banda (Fig. S6). Decapod crustaceans possess species-specific optimal temperatures for survival and growth (McLay 2015; Pörtner et al. 2017; Yamamoto et al. 2017). Thus, the local temperature conditions might affect the growth and overwintering success of coenobitid juveniles. The MLT values of the juveniles estimated by the laboratory experiment of Sanda et al. (2019) under the reducing temperature regime over a period of approximately three weeks were 7.9°C and 10.2°C for *C. purpureus* and *C. rugosus*, respectively. In our laboratory experiment that simulated the *in situ* daily temperature fluctuations (~8–15°C) during the early overwintering period, all *C. rugosus* juveniles died, whereas almost all *C. purpureus* juveniles survived during the nine-day period. Additionally, all *C. rugosus* juveniles had died on the Boso Peninsula where the winter temperature was frequently below 10°C (Table S7), and all *C. purpureus* juveniles had died at Banda where winter temperature was generally below 8°C (Table S7). Thus, temperature levels of 8°C and 10°C might be the low-temperature tolerance limits of juveniles of *C. purpureus* and *C. rugosus*, respectively. At Shirosaki, juveniles appeared to grow from February to March; this might be because of the death of smaller crabs.

Considering the abundance of reproductive populations of coenobitid crabs in the Ryukyu

Archipelago, it is thought that larvae of coenobitid crabs disperse broadly in the southern islands and the Pacific coasts of Japan via the Kuroshio Current and its countercurrents. Then, we hypothesize that after landing, early juveniles might die depending on the species-specific low-temperature tolerance properties during the overwintering period, leading to the current biogeographical pattern of coenobitid species. Our results supported this hypothesis; however, only two species, *C. purpureus* and *C. rugosus*, appeared in the newly landed early juvenile collections, even though six coenobitid species commonly occur in the southern islands of Japan. Among the coenobitid crabs, *C. purpureus* and *C. rugosus* are dominant species in the northern and southern Ryukyu Archipelago, respectively (KPBE 1987; OPBE 1987; Fujikawa et al. 2017; Sanda et al. 2018a, b). A large population size might increase the chance of these two species of colonizing the Pacific coast of Japan via the Kuroshio Current during the pelagic larval stage.

Recruitment fluctuation of land hermit crabs

We conducted field surveys at four sites in successive three years and demonstrated that the abundance of new recruits varied among survey sites and years (Fig. 3). The number of newly landed juveniles tended to be large at two sites, Banda and Okinoshima, located in Tateyama Bay compared with the other two sites, Shirosaki and Katsuura, located on the coast facing the Pacific, and it was larger in 2012 than 2013 and 2014. Tateyama Bay is the most northern distribution area of tropical reef corals (Hagiwara 2003; Yamano and Namizaki 2009; Yamano et al. 2011). Larvae of southern marine organisms are transported from warmer to cooler latitudes via the Kuroshio Current (Veron and Minchin 1992; Iida et al. 2010; Soeparno et al. 2012; He et al. 2015; Yuhara et al. 2017; Chang et al. 2018), and the opportunity to settle the Tateyama Bay by these larvae might increase through the local tidal current system near or in the bay. The Kuroshio Current pathway temporarily and seasonally varied in the Pacific region of Japan (Douglass et al. 2012), and its variations change the hydrographic conditions that in turn affect the formation of fishing grounds as well as the recruitment and reproduction of various fishery resources around the Kuroshio and adjacent waters (Ogawa and Wakabayashi 1992; Nakata et al. 2000). Here, we summarized the distance from the Cape Nojimizaki (34°54'N, 139°53'E) (Fig. 1), which is the southernmost location of the Boso Peninsula, to the center of the Kuroshio Current and its directions in July, August, September and October in 2012, 2013 and 2014 using a database from the Hydrographic and Oceanographic Department, Japan Coast Guard (<https://www1.kaiho.mlit.go.jp/KANKYO/KAIYO/qboc/kurosio-num.html>) (Table S9). In 2013, and 2014, when the populations of new recruits were small, the Kuroshio Current tended to flow in a more offshore direction (2013), and its pathway direction was frequently east or east-southeast

(2013 and 2014) compared to the 2012 profile. Although there is no information on how the directions of the Kuroshio Current off Cape Nojimazaki affect the local tidal current system near the coast of the Boso Peninsula, our surveys and analyses suggest that variations of the Kuroshio Current pathway might affect the larval transport and settlement of coenobitid crabs on the Boso Peninsula.

Global warming and land hermit crab populations

Global warming should affect the biogeography of ectotherms (Pörtner 2001; Gunderson and Stillman 2015). Intertidal and land hermit crabs often have genetic population differentiation among regions in the northwestern Pacific (Hamasaki et al. 2017a; Jung et al. 2018) and different lineages may have different thermal tolerance. Increasing temperature from global warming may result in altering the biogeography of those genetic lineages.

Adult *C. purpureus* appeared to have the weak low-temperature tolerance abilities compared with juveniles because they died after exposure for eight days, but juvenile *C. purpureus* could survive for the same period in our laboratory experiment under cyclic low temperature conditions (Figs. 5, 6). Although the physiological mechanisms of the different low-temperature tolerance properties between adult and juvenile crabs are unknown, the weak low-temperature tolerance ability of adult *C. purpureus* might be responsible for the small population size of *C. purpureus* on the Boso Peninsula. Populations of *C. purpureus* may increase on the Boso Peninsula because the air and sea-surface temperatures have increased in the whole country of Japan (Japan Meteorological Agency; http://www.data.jma.go.jp/cpdinfo/index_temp.html). Monitoring the populations of *C. purpureus* on the Boso Peninsula would assist us in inferring the degree of progress of global warming. Furthermore, revealing the effects of temperature on the reproduction of adult crabs would also assist us in predicting the establishment of the self-recruitment population of *C. purpureus* under a global warming scenario.

CONCLUSIONS

Our field surveys and laboratory experiments supported the hypothesis that early juveniles of coenobitid crabs might die depending on the species-specific low-temperature tolerance properties during the overwintering period on the Pacific coast of Japan. Recruitment of two land hermit crab species, *C. purpureus* and *C. rugosus*, occurred and *C. purpureus* was dominant in new recruits on the coast of the Boso Peninsula, the northernmost region where marine biodiversity is directly

influenced by the Kuroshio Current. *C. purpureus* successfully overwintered there depending on the low-temperature tolerance trait and grew to the maturity size. The present study thus highlighted the frontier for expanding the northern geographical distribution of land hermit crab populations by the colonization and overwintering success of *C. purpureus*. Our field study is the important first step for inferring the degree of progress of global warming through investigating the population dynamics of coenobitid crabs on the northern limit of their geographical distributions.

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Authors' contribution: KH designed the study. TS and KH performed the field and laboratory studies. TS, KH, SD, and SK prepared the manuscript. All authors approved the final manuscript.

Competing interests: The authors declare that they have no conflicts of interest.

Availability of data and materials: All the data are provided within the manuscript and supplementary materials.

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Ethics approval consent to participate: The present study complies with current Japanese laws.

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Supplementary Materials

Fig. S1. Google Earth photographs showing the survey sites on the coast of Boso Peninsula, Japan. Banda (34°58'N, 139°46'E) (a), Okinoshima (34°59'N, 139°49'E) (b), Shirosaki (35°7'N, 140°10'E) (c), and Katsuura (35°8'N, 140°17'E) (d). Broken lines indicate the survey scopes. The locations where many coenobitid crabs were found are indicated by white circles, and their photos are imposed in each site panel. Horizontal white lines are scale bars (100 m). (download)

Fig. S2. Relationship between dactylus length of the third pereopod and shield length of juveniles of coenobitid crabs *Coenobita purpureus* and *C. rugosus*. (download)

Fig. S3. Test temperature profiles in experiment 1 to evaluate the low-temperature tolerance ability of adults of *Coenobita purpureus* and *C. rugosus* under constant low-temperature conditions. Test temperature levels were 2°C (a), 4°C (b, c), 6°C (d, e), 8°C (f, g) and 10°C (h, i), and the test trial was conducted twice for each level except for 2°C. The air temperature was recorded every 15 min with a data logger (Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan). (download)

Fig. S4. *In situ* temperature fluctuation during the early wintering period at Okinoshima (a) on the Boso Peninsula, Japan, and test temperature profiles in experiment 2 to evaluate the low-temperature tolerance ability of adults (b, c) and juveniles (d) of *Coenobita purpureus* and *C. rugosus* under the cyclic low-temperature conditions that simulated the *in situ* daily temperature fluctuation. The air temperature was recorded every 15 min with a data logger (Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan). (download)

Fig. S5A. Size-frequency distributions of coenobitid crabs at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan from August 2012 (a) to July 2013 (l). The number of crabs measured is shown in parentheses. (download)

Fig. S5B. Size-frequency distributions of coenobitid crabs at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan from August 2013 (a) to July 2014 (h). The number of crabs measured is shown in parentheses. (download)

Fig. S5C. Size-frequency distributions of coenobitid crabs at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan from August (a) to December 2014 (e). The number of crabs measured is shown in parentheses. (download)

Fig. S6. Daily mean air temperatures measured at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan during the overwintering period from December 1, 2013 to March 11, 2014 (a), and from November 1 to December 22, 2014 (b). (download)

Fig. S7. Monthly mean air temperatures measured at the meteorological station in Tateyama (34°59.2'N, 139°51.9'E) and Shirahama (33°39.7'N, 135°21.8'E), Japan (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). (download)

Table S1. Survey sites, sampling months, and number of specimens for genetically identifying the species of newly landed juvenile crabs belonging to the genus *Coenobita* on the coast of Boso

Peninsula, Japan. (download)

Table S2. Shield length of adult crabs of *Coenobita purpureus* and *C. rugosus* used in experiment 1 to evaluate low-temperature tolerance abilities under constant low-temperature conditions.

(download)

Table S3. Shield length of juvenile or adult crabs of *Coenobita purpureus* and *C. rugosus* used in experiment 2 to evaluate low-temperature tolerance abilities under cyclic low temperature conditions that simulated the *in situ* daily temperature fluctuation. (download)

Table S4. Mean air temperatures during the accumulation, test and recovery periods in experiment 2 to evaluate low-temperature tolerance abilities of adults of *Coenobita purpureus* and *C. rugosus* under constant low temperature conditions. (download)

Table S5. Number of age-0 (A0), age-1< (A1), and dead coenobitid crabs counted at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan.

(download)

Table S6. Shield length of age-0 juveniles of coenobitid crabs at four survey sites (Banda, Okinoshika, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan. (download)

Table S7. Average values of daily mean, minimum and maximum temperatures for the 10-day interval measured during the early overwintering period of coenobitid crabs at four survey sites (Banda, Okinoshima, Shirosaki, and Katsuura) on the coast of the Boso Peninsula, Japan.

(download)

Table S8. Parameter estimates of logistic equations [$y = 1/(1+e^{-(a+bx)})$] describing the relationship between temperatures and survival rates of adult crabs of *Coenobita purpureus* and *C. rugosus* in experiment 1 under constant low-temperature conditions. (download)

Table S9. Distance from the Cape Nojimazaki (34°54'N, 139°53'E), the southernmost place of the Boso Peninsula, Japan to the center of the Kuroshio Current and its directions in July, August, September and October in 2012, 2013 and 2014. (download)