

Effect of temperature on larval survival, development and duration of six terrestrial hermit crab species under laboratory conditions

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Abstract

Temperature is an important environmental factor affecting the larval survival, development and duration of decapod crustaceans. We investigated the effect of temperature on larval performance in six terrestrial hermit crab species (genera *Birgus* and *Coenobita*): *B. latro*, *C. brevimanus*, *C. cavipes*, *C. purpureus*, *C. rugosus*, and *C. violascens*. Larvae were cultured at six temperature levels between ~19 and 34 °C. Larvae could not survive to the megalopal stage at temperatures below 20 °C. Megalopae appeared at temperatures above ~22–23 °C, and survival rates to the megalopal stage were high at ~25–31 °C and tended to decline over ~32 °C. Intra- and interspecific variations were found in the developmental pathways to the megalopal stage: 4 zoeal stages in *B. latro*, 4–8 zoeal stages in *C. cavipes* and 4 or 5 zoeal stages in the other *Coenobita* species. The proportions of larvae that completed the shorter developmental pathways tended to increase with increasing temperature in each species. Total zoeal duration tended to decrease with increasing temperature in all species, and *C. cavipes*, with prolonged developmental pathways, exhibited the longest developmental periods to the megalopal stage. The lower threshold temperature for larval development was estimated to be 16.4–19.3 °C based on the heat summation theory equation. Thus, larvae of coenobitid crabs are not able to develop and survive at low-temperature conditions below 20 °C, exhibiting typical thermal adaptation of subtropical and tropical species.

Key words: Coconut crab; land hermit crab; larval developmental pathway; larval dispersal; thermal adaptation

Introduction

Terrestrial hermit crabs of the family Coenobitidae comprise two genera, *Coenobita* Latreille 1829, with approximately 17 species, and *Birgus* Leach 1816, with only one species: *B. latro* (Linnaeus 1767) (Hartnoll 1988; Poupin 1996; McLaughlin et al. 2010; Rahayu et al. 2016). Coenobitid crabs are mainly distributed in subtropical and tropical coastal regions (Hartnoll 1988). They are scavengers in coastal ecosystems (Page and Willason 1983; Thacker 1996), and *B. latro* and *Coenobita* spp. are used as food and ornamental animals by humans, respectively (Brown and Fielder 1991; Pavia 2006).

Coenobitid crabs are terrestrial except during the larval phase. After hatching on shores, coenobitid larvae spend their pelagic life through several zoeal stages to megalopae in the sea (Hartnoll 1988; Hamasaki et al. 2015a). After settlement, the megalopae acquire empty gastropod shells and then migrate onto land (Reese 1968; Harvey 1992; Brodie 1999; Hamasaki et al. 2011, 2015b). Laboratory experiments demonstrated that early zoeae and megalopae were euryhaline and later zoeae were stenohaline in six coenobitid species, *B. latro*, *C. brevimanus* Dana 1852, *C. cavipes* Stimpson 1858, *C. purpureus* Stimpson 1858, *C. rugosus* H. Milne-Edwards 1837, and *C.*

violascens Heller 1862, which occur in Japan (Hamasaki et al. 2018). Thus, it has been suggested that after hatching in estuaries with unstable and low-salinity conditions, coenobitid zoeae might disperse through coastal or offshore areas with stable and high-salinity conditions, and megalopae finally return to the estuarine habitat to initiate the benthic part of the life cycle (Hamasaki et al. 2018). Accordingly, zoeae and megalopae of terrestrial hermit crabs play important roles in dispersal and recruitment processes in the sea, respectively.

Temperature is one of the most important environmental factors known to affect the larval survival, development and duration of decapod crustaceans (Anger 2001), and seawater temperature fluctuates temporally and spatially. Therefore, information on larval performance under different temperature conditions is essential for a better understanding of the ecological processes of coenobitid species in the sea, including larval survival and dispersal, population connectivity, recruitment dynamics and geographical distribution. However, the influence of temperature on the larval performance of coenobitid species remains largely unknown. To date, the zoeal duration and number of zoeal stages, i.e., the developmental pathway leading to the megalopal stage, based on laboratory cultures at particular temperatures have been reported for 10 coenobitid species (Hamasaki et al. 2015a), and only laboratory culture using *B. latro* has been conducted under different temperature conditions (Hamasaki et al. 2009).

Our objective in the present study was to investigate the influence of temperature on larval survival, developmental pathway and duration in

terrestrial hermit crabs by culturing larvae of six coenobitid species, *B. latro*, *C. brevimanus*, *C. cavipes*, *C. purpureus*, *C. rugosus*, and *C. violascens*, that occur in Japan.

Materials and methods

Larval source

Culture experiments were conducted in a laboratory at Tokyo University of Marine Science and Technology, Tokyo, in 2012, 2014 and 2015. Oviparous females of six coenobitid species, *B. latro*, *C. brevimanus*, *C. cavipes*, *C. purpureus*, *C. rugosus*, and *C. violascens*, were captured by hand during late June to early July on Hatomajima Island (24°28'N, 123°49'E) or Ishigakijima Island (24°23–31'N, 124°07–18'E), Okinawa Prefecture, Japan. They were transported to the laboratory, where the air temperature was controlled at ~27–28 °C, which is equivalent to the summer temperature during the reproductive season of coenobitid crabs in natural habitats. The crabs were then maintained in tanks equipped with simulated land and sea areas (artificial seawater, 34 ppt salinity; Sealife, Marinetech Co. Ltd., Tokyo, Japan) according to the methods of Hamasaki et al. (2009) and Hamasaki (2011). Larval hatching occurred during early to late July, and newly hatched zoeae from a single female of each species were used for the larval culture experiments. The larval hatching date of each species are shown in supplementary Table S1 in the electronic supplementary material (<http://aquaanimal.net/cgi-bin/appendix/HamasakiEM.pdf>).

All species of the genus *Coenobita* in Japan are recognized collectively as a Natural Monument Animal to promote their conservation. *Coenobita*

spp., therefore, were collected and cultured under permission (license certificate nos. 4-1997 and 4-2058) from the Agency for Cultural Affairs, Ministry of Education, Culture, Sports, Science and Technology of Japan. In addition, *B. latro* is listed as “vulnerable” in the Red Data Book of the Ministry of the Environment of Japan. Therefore, the wild crabs used in the present study were returned to their natural habitats after the experiments were completed.

Larval culture experiments

Larvae were cultured under six different temperature levels, ~19–20 °C, 22–23 °C, 25–26 °C, 27–28 °C, 29–31 °C, and 32–34 °C, using temperature-controlled incubation chambers with a photoperiod cycle of 14-h light and 10-h dark (MT1-201, Tokyo Rikakikai Co. Ltd., Tokyo, Japan). Rearing temperatures were recorded every 30 min during larval culture periods using data loggers (Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan) placed in the larval culture containers (see supplementary Table S1 for the mean ± standard deviation values of larval rearing temperatures for each species).

Newly hatched larvae (stage 1 zoeae, total of 36) of each species were housed individually in the wells of 6 six-well cell culture plates, which contained 10 ml artificial seawater (34 ppt salinity) in each well. Larvae were fed zooplankton including the rotifer *Brachionus plicatilis* species complex and *Artemia* sp. The rotifers were cultured with the phytoplankton *Chlorella vulgaris* containing n-3 highly unsaturated fatty acids (n-3HUFAs) in its cells (Super Chlorella V12, Chlorella Industry, Tokyo, Japan) and then fed to

larvae at 40 individuals ml⁻¹. *Artemia* (Utah strain) aged 2 days were enriched with a commercial feed containing n-3HUFAs (SCP, Chlorella Industry) for 4 h and then given to larvae at 2 individuals/ml⁻¹. The n-3HUFAs are known to be essential fatty acids for the larval survival and development of some decapod crustaceans (Suprayudi et al. 2004). Each morning, larvae were transferred to clean culture wells with fresh seawater and food using a large-mouthed pipette, and the numbers of live and dead larvae were recorded. Each larval moulting was determined by the presence of an exuvia. Larval rearing was terminated when all surviving larvae had moulted to the megalopal stage. Some (range: 1–10, but mostly 0 or 1) zoeal larvae were lost accidentally during the culture operations, and these larvae were excluded from the data analysis (see supplementary Table S1 for the actual numbers of stage 1 zoeae used for each temperature level in each species).

Statistical analysis

Statistical analyses were performed using R statistical software (R3.6.2; R Core Team 2019) at a 5 % significance level. To evaluate the influence of temperature on larval survival until metamorphosis into the megalopal stage, we used a bias-reduced generalized linear model (BRGLM) with a binomial distribution, i.e., a logistic model, and the coefficients of a logistic equation (with standard errors; z-values with probabilities) were estimated using the `brglm` function (logit link) implemented in the `brglm` package (Kosmidis 2019). In the BRGLM analysis, binary survival (1) or death (0) was a response variable, and

temperature was a continuous explanatory variable. The larval developmental pathway varied among culture temperatures in all of the coenobitid species except *B. latro* (see the Results section). BRGLM analysis was also performed to determine whether larvae metamorphosed into megalopae through shorter (1) or longer (0) developmental pathways. The relationship between temperature and larval survival rate was represented by a convex curve (see the Results section); therefore, a quadratic term for temperature was also included as an explanatory variable in the BRGLM analysis for survival (Fletcher and Fortin 2018).

The relationship between mean rearing total

zoal duration (D), was fitted with the following equation: $D = a/(T - b)$. This equation, known as Réaumur's Law, is part of the theory of temperature (T) and the number of days required from hatching to reach the megalopal stage, i.e., heat summation; the parameters a and b are the so-called 'thermal constant' and 'lower threshold temperature (LTT)' for development, respectively (Hamasaki 2003). The thermal constant is the summation of the effective temperature for development ($>$ threshold temperature) up to a selected biological end point. The parameters were estimated using a nonlinear ordinary least-squares method and evaluated with t-tests.

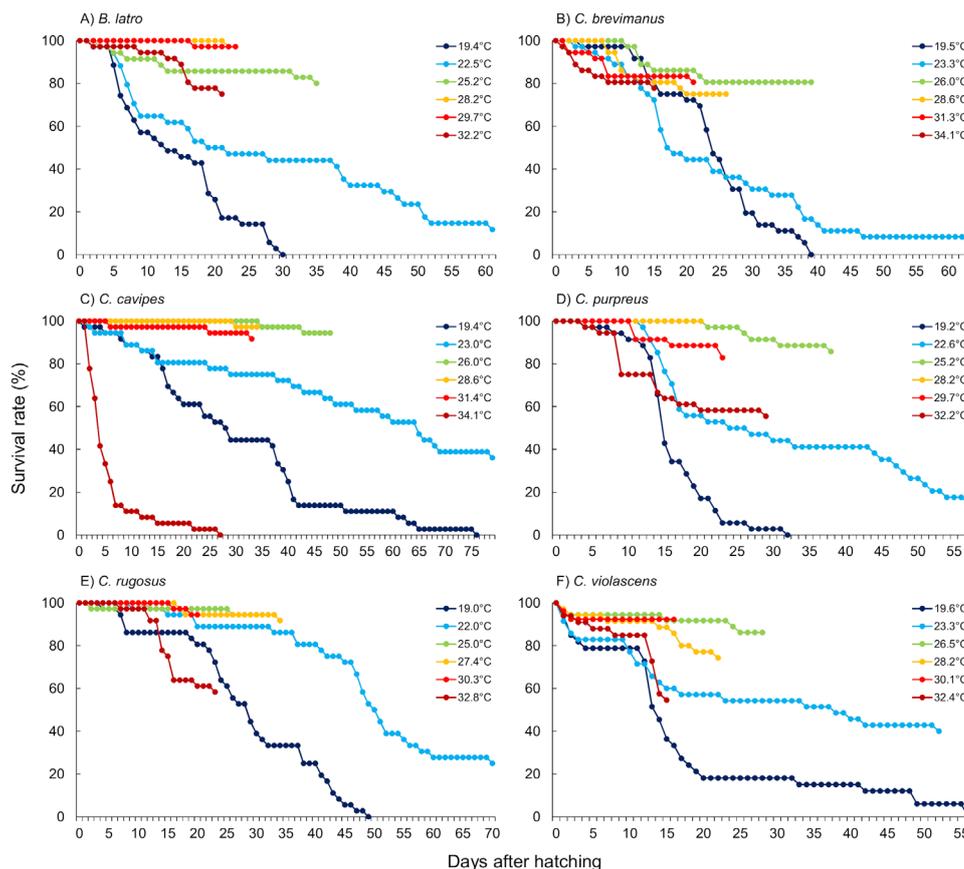


Fig. 1. Changes in the survival rate in relation to days after hatching for larvae reared at six different temperatures for six coenobitid species: *Birgus latro* (A), *Coenobita brevimanus* (B), *C. cavipes* (C), *C. purpureus* (D), *C. rugosus* (E), and *C. violascens* (F). Larvae were cultured until all surviving larvae had moulted to the megalopal stage. Mean rearing temperatures are shown in each graph.

Results

Larval survival

Larval survival varied among culture temperatures in each coenobitid species (Fig. 1). The stage 1 zoeae of *B. latro*, *C. brevimanus* and *C. purpureus* could not moult at 19.4 °C, 19.5 °C and 19.2 °C, and all larvae died 30, 39, and 32 days after hatching, respectively. A small proportion of the larvae of *C. cavipes*, *C. rugosus* and *C. violascens* moulted to stage 5, stage 2 and stage 5 zoeae at 19.4 °C, 19.0 °C and 19.6 °C, but all died 76, 49, and 56 days after hatching, respectively (Fig. 1 and see supplementary Figs. S1–S6 for changes in the number of larvae in relation to days after hatching for different larval stages of the respective species). Megalopae appeared at temperatures above ~22–

23 °C (Fig. 2 and Figs. S1–S6); survival rates to metamorphosis into the megalopal stage were high at ~25–31 °C and tended to decline over ~32 °C, although *C. brevimanus* larvae exhibited a high survival rate even at 34 °C, whereas all *C. cavipes* larvae died 27 days after hatching at 34 °C. Overall, the relationship between temperature and larval survival rate was represented by a convex curve in each species (Fig. 2), and coefficient estimates of the logistic equation evaluating the temperature effect on larval survival were statistically significant in all species (Table 1).

Larval development

Larval *B. latro* metamorphosed into megalopae from stage 4 zoeae regardless of culture tempera-

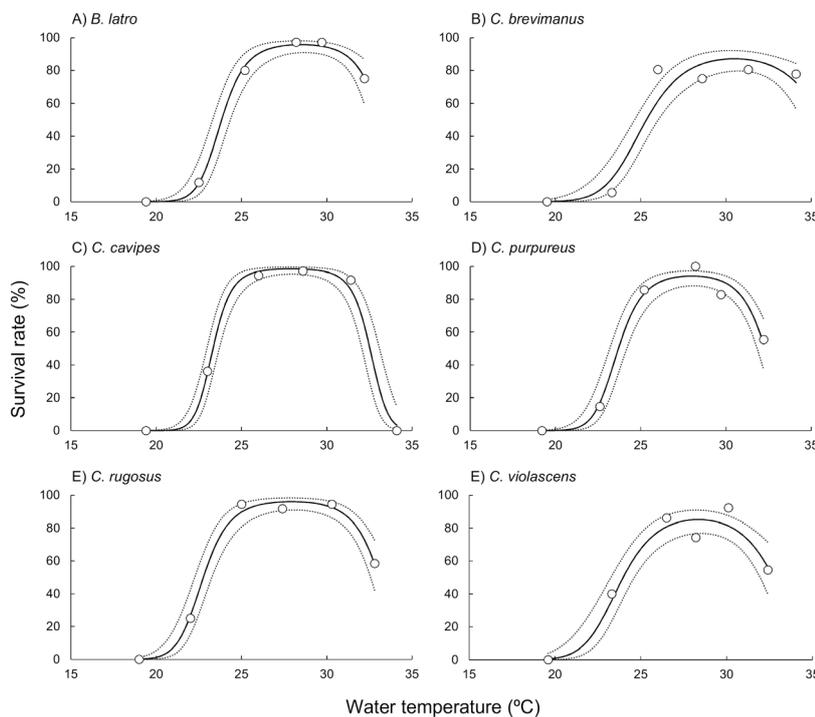


Fig. 2. Relationships between mean rearing temperature and larval survival rate to the megalopal stage in six coenobitid species: *Birgus latro* (A), *Coenobita brevimanus* (B), *C. cavipes* (C), *C. purpureus* (D), *C. rugosus* (E), and *C. violascens* (F). Observed survival rates were calculated as (number of larvae metamorphosed into the megalopal stage)/(initial number of stage-1 zoeae) and are shown by open circles. Survival curves were drawn based on the logistic equations shown in Table 1. Solid and dotted curves indicate the fitted values and their 95 % confidence intervals, respectively.

Table 1. Coefficient estimates with standard errors (SE) of the logistic equation [$y = 1/(1 + \exp(-(a + bx + cx^2)))$] used to evaluate the effect of rearing temperature (x) on larval survival (y) until metamorphosis into the megalopal stage in six coenobitid species of the genera *Birgus* and *Coenobita*.

Species	n	Coefficient	Estimate	SE	z value	p value
<i>Birgus latro</i>	211	<i>a</i>	-114.2744	18.9033	-6.045	<0.0001
		<i>b</i>	8.2434	1.3865	5.945	<0.0001
		<i>c</i>	-0.1447	0.0250	-5.789	<0.0001
<i>Coenobita brevimanus</i>	216	<i>a</i>	-65.0191	12.8548	-5.058	<0.0001
		<i>b</i>	4.3908	0.8974	4.893	<0.0001
		<i>c</i>	-0.0720	0.0154	-4.665	<0.0001
<i>Coenobita cavipes</i>	216	<i>a</i>	-150.6792	21.3536	-7.056	<0.0001
		<i>b</i>	11.0913	1.5797	7.021	<0.0001
		<i>c</i>	-0.1986	0.0285	-6.959	<0.0001
<i>Coenobita purpureus</i>	210	<i>a</i>	-115.3319	16.9730	-6.795	<0.0001
		<i>b</i>	8.4409	1.2479	6.764	<0.0001
		<i>c</i>	-0.1508	0.0225	-6.691	<0.0001
<i>Coenobita rugosus</i>	216	<i>a</i>	-90.3807	13.5241	-6.683	<0.0001
		<i>b</i>	6.7029	1.0105	6.633	<0.0001
		<i>c</i>	-0.1200	0.0184	-6.534	<0.0001
<i>Coenobita violascens</i>	198	<i>a</i>	-71.5700	13.4447	-5.323	<0.0001
		<i>b</i>	5.1729	0.9828	5.263	<0.0001
		<i>c</i>	-0.0912	0.0177	-5.150	<0.0001

n, number of larvae.

ture, whereas intraspecific variations in the developmental pathways were found in other species (Fig. 3). Developmental pathways were highly variable in *C. cavipes* larvae between 4–8 zoeal stages, and the larvae were tentatively classified as having a shorter pathway (4–6 zoeal stages, mostly 5–6) or a longer pathway (7–8 zoeal stages). In other *Coenobita* species, larvae moulted to the megalopal stage through stage 4 (shorter pathway) or 5 zoeae (longer pathway), although one stage-6 zoea of *C. brevimanus* appeared but died without further moulting at 23.3 °C. The proportions of larvae that passed through the shorter developmental pathways tended to increase

with increasing temperature (Fig. 3), and coefficient estimates from the logistic equation evaluating the temperature effect on developmental pathway were statistically significant in all species (Table 2).

Larval duration

Total zoeal duration tended to decrease with increasing temperature in all species (Fig. 4). The LTT for larval development was estimated to be 16.4–19.3 °C (coefficient *b* shown in Table 3), and it was slightly lower in *B. latro* (16.4 °C). The estimate of the thermal constant for larval development ranged between 150 and 320 degree

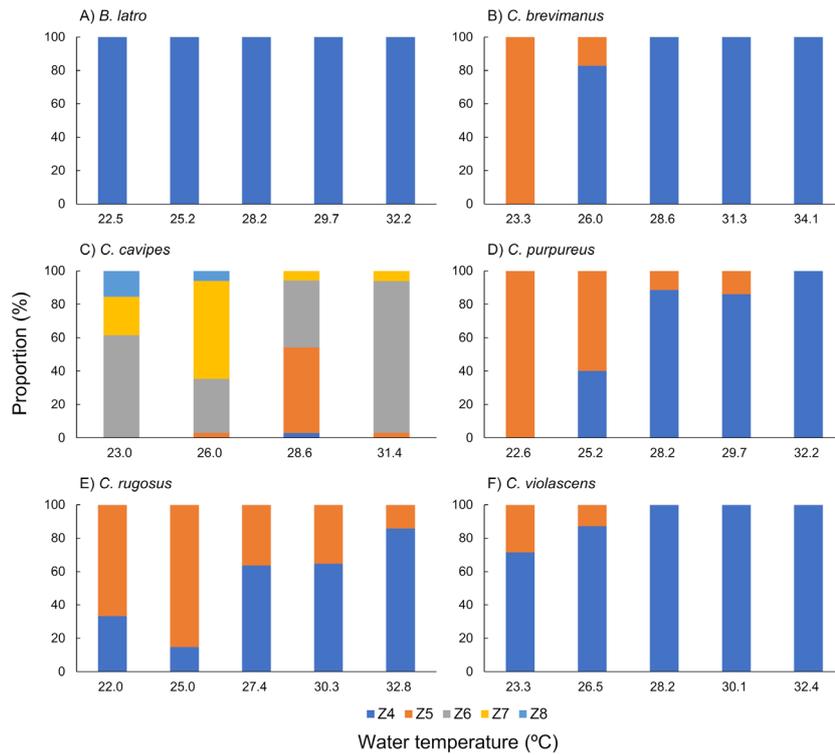


Fig. 3. Composition of larval developmental pathways under different temperatures in six coenobitid species: *Birgus latro* (A), *Coenobita brevimanus* (B), *C. cavipes* (C), *C. purpureus* (D), *C. rugosus* (E), and *C. violascens* (F). Larval developmental pathway: number of zoeal stages required to metamorphose into the megalopal stage (Z4–Z8, 4–8 zoeal stages).

Table 2. Coefficient estimates with standard errors (SE) of the logistic equation $[y = 1/(1 + \exp(-(a + bx))]$ used to evaluate the effect of rearing temperature (x) on the incidence of metamorphosis into the megalopal stage (y) through shorter larval developmental pathways in five *Coenobita* species.

Species	Shorter developmental pathway	n	Coefficient	Estimate	SE	z value	p value
<i>Coenobita brevimanus</i>	Z4	115	<i>a</i>	-31.0335	13.9116	-2.231	0.0257
			<i>b</i>	1.2504	0.5346	2.339	0.0193
<i>Coenobita cavipes</i>	Z4–Z6	115	<i>a</i>	-10.0043	2.5997	-3.848	0.0001
			<i>b</i>	0.4009	0.0962	4.170	<0.0001
<i>Coenobita purpureus</i>	Z4	119	<i>a</i>	-16.8610	3.4072	-4.949	<0.0001
			<i>b</i>	0.6524	0.1264	5.161	<0.0001
<i>Coenobita rugosus</i>	Z4	131	<i>a</i>	-8.5917	1.9176	-4.481	<0.0001
			<i>b</i>	0.3111	0.0684	4.548	<0.0001
<i>Coenobita violascens</i>	Z4	113	<i>a</i>	-12.0132	4.4165	-2.720	0.0065
			<i>b</i>	0.5438	0.1729	3.145	0.0017

Larval developmental pathway, number of zoeal stages required to metamorphose into the megalopal stage (Z4–6, 4–6 zoeal stages). n, number of larvae.

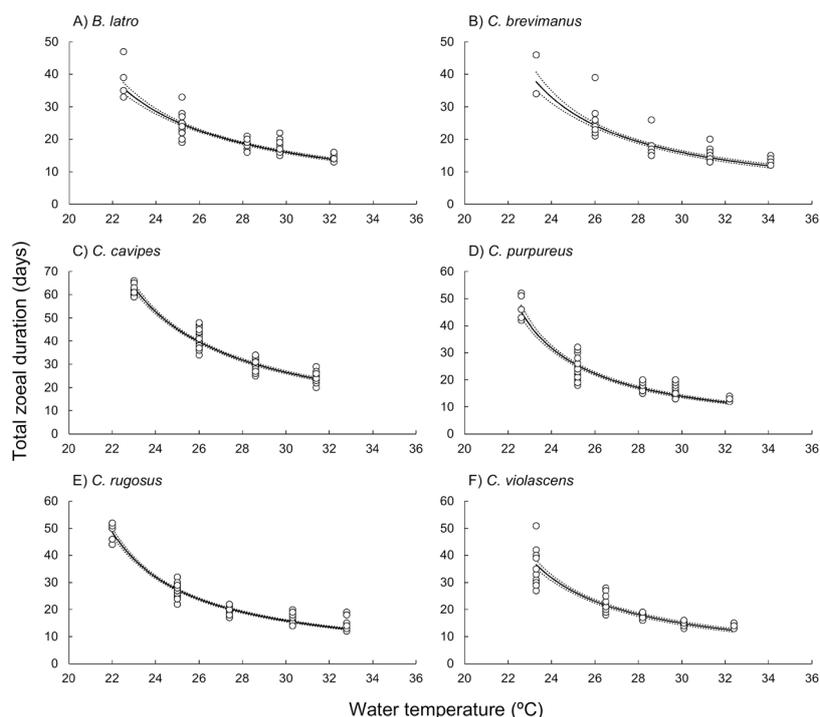


Fig. 4. Relationships between mean rearing temperature and total zoeal duration from hatching to metamorphosing to the megalopal stage in six coenobitid species: *Birgus latro* (A), *Coenobita brevimanus* (B), *C. cavipes* (C), *C. purpureus* (D), *C. rugosus* (E), and *C. violascens* (F). Zoeal duration curves were drawn based on the heat summation theory equations shown in Table 3. Solid and dotted curves indicate the fitted values and their 95 % confidence intervals, respectively.

days (coefficient a shown in Table 3), and it was highest in *C. cavipes* with a prolonged zoeal developmental period (Fig. 5).

Discussion

Larval survival and development

The present study demonstrated that temperatures significantly influenced larval survival and development in six coenobitid species. At low-temperature conditions below 20 °C, some larvae survived for a month or more but did not reach the megalopal stage (Figs. 1 and 2). Larvae survived to the megalopal stage at temperatures above ~22–23 °C, and survival rates were high at ~25–31 °C (Fig. 2). Hamasaki et al. (2009) con-

ducted group culture of *B. latro* larvae by stocking 30 zoeae in three replicated 1-l beakers at six different temperatures between ~19 and 32 °C and reported the mean survival rates to the megalopal stage as 0 % (18.9 °C), 1 % (21.3 °C), 57 % (24.6 °C), 86 % (27.0 °C), 82 % (29.8 °C), and 56 % (32.4 °C), similar to those in the present study (Fig. 2A).

In the present study, the total zoeal duration of the coenobitids decreased with increasing temperature, as shown for many decapod crustacean species (Anger 2001), and the LTT for larval development was estimated to be 16.4 °C for *B. latro* and 17.9–19.3 °C for *Coenobita* species from the heat summation theory equation as ap-

Table 3. Coefficient estimates with standard errors (SE) of the heat summation theory equation [$D = a/(T - b)$] describing the relationship between mean temperature (T , °C) and days required from hatching to metamorphosis into the megalopal stage (D , days) of larvae cultured at different water temperatures for six coenobitid species of the genera *Birgus* and *Coenobita*.

Species	n	Coefficient	Estimate	SE	t value	p value
<i>Birgus latro</i>	128	<i>a</i>	218.0148	7.6297	28.57	<0.0001
		<i>b</i>	16.3887	0.3394	48.28	<0.0001
<i>Coenobita brevimanus</i>	115	<i>a</i>	185.3942	8.6465	21.44	<0.0001
		<i>b</i>	18.3818	0.3916	46.95	<0.0001
<i>Coenobita cavipes</i>	115	<i>a</i>	321.5156	7.9339	40.52	<0.0001
		<i>b</i>	17.9016	0.1725	103.78	<0.0001
<i>Coenobita purpureus</i>	119	<i>a</i>	149.7410	4.8640	30.79	<0.0001
		<i>b</i>	19.2830	0.1740	110.81	<0.0001
<i>Coenobita rugosus</i>	131	<i>a</i>	187.7946	4.3767	42.91	<0.0001
		<i>b</i>	18.1364	0.1334	136	<0.0001
<i>Coenobita violascens</i>	113	<i>a</i>	169.1266	7.0586	23.96	<0.0001
		<i>b</i>	18.6744	0.2617	71.37	<0.0001

n, number of larvae.

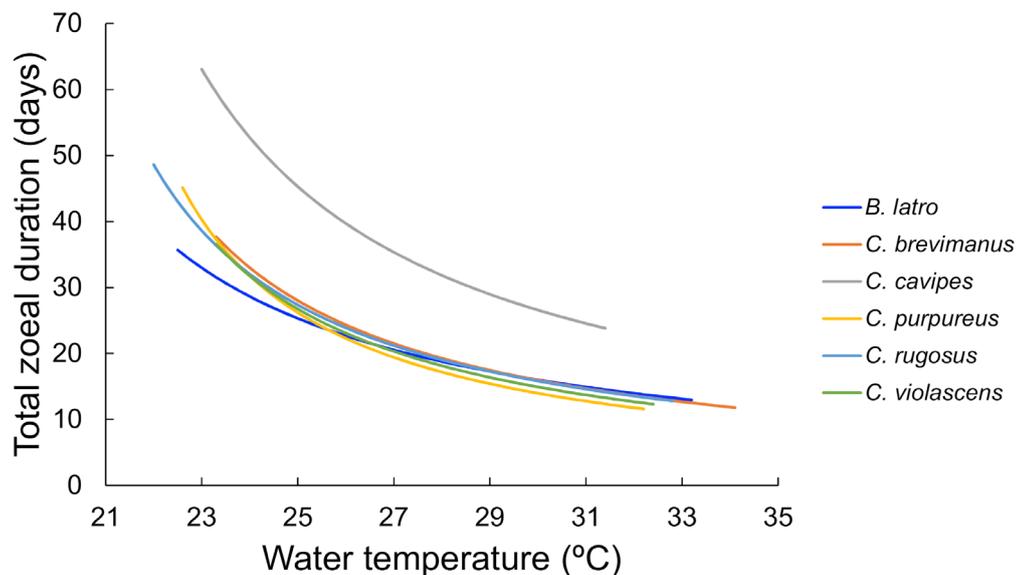


Fig. 5. Interspecific comparison of total zoeal duration in relation to temperature in six coenobitid species: *Birgus latro*, *Coenobita brevimanus*, *C. cavipes*, *C. purpureus*, *C. rugosus*, and *C. violascens*. Zoeal duration curves were drawn based on the heat summation theory equations shown in Table 3.

plied to the relationship between temperature and total zoeal duration (Table 3). Hamasaki et al. (2009) also estimated the LTT for zoeal development of *B. latro* as ~18 °C. Accordingly,

larvae of coenobitid crabs are not able to develop and survive at low-temperature conditions below 20 °C, exhibiting typical thermal adaptation of subtropical and tropical species (Anger 2001).

Hamasaki et al. (2016) estimated the LTTs of 12.7–14.5 °C for embryonic development of the six coenobitid species as observed in the present study. Thus, the LTT for development was lower for embryos than for zoeal larvae. This is a common finding because the embryonic developmental period precedes that of larvae during the reproductive season (Hamasaki et al. 2016).

Larval developmental pathway

Intraspecific variability in larval developmental pathways has been observed for decapod crustaceans (Knowlton 1974; Gore 1985; Anger 2001, 2006). The causes of the variability have been attributed to genetic and maternal factors and to environmental stress, such as unfavourable salinities and temperatures and limited nutritional conditions (Anger 2001; Zeng et al. 2004). Laboratory studies have also reported intraspecific variability in larval developmental pathways of coenobitid species (Hamasaki et al. 2015a), but little is known about the causes of the variability. In the present study, larvae required more zoeal stages before reaching the megalopal stage under the lower-temperature conditions (Fig. 3). In our larval culture experiments, all *B. latro* larvae metamorphosed into megalopae through stage-4 zoeae, but Hamasaki et al. (2009) found that stage-5 zoeae that died without further moulting occurred in groups reared at low temperatures below 25 °C. Thus, temperature is an important environmental factor inducing intraspecific variation in the larval developmental pathways of coenobitid crabs.

The interspecific variability in larval developmental pathways found in the present study

was similar to that previously reported for coenobitid species (Hamasaki et al. 2015a); *C. cavipes* exhibited prolonged developmental pathways (mostly 5–7 zoeal stages) compared with those of the other species (*B. latro*, 4 zoeal stages; other *Coenobita* species, 4 or 5 zoeal stages). Hamasaki et al. (2015a) revealed that interspecific variation in body size was large in newly hatched larvae but small in megalopae, the newly hatched larvae of *C. cavipes* were the smallest among the coenobitids, and the zoeae of this species exhibited smaller growth increments at moulting; accordingly, the authors suggested that *C. cavipes* larvae might require a prolonged developmental pathway, i.e., a prolonged zoeal developmental period compared with that of other coenobitid species to achieve a given size at the megalopal stage. Smaller growth increments might also occur under unfavourable low-temperature conditions, resulting in intraspecific variability in the larval developmental pathways of coenobitid crabs.

In the present study, the larval developmental pathway of *B. latro* was stable and the shortest (4 zoeal stages) among six coenobitid species regardless of culture temperature. The newly hatched larvae of *B. latro* were the largest among six coenobitid species (Hamasaki et al. 2015a); therefore, *B. latro* larvae might be able to achieve a given size at the megalopal stage through a shortened developmental pathway.

Larval dynamics in the ocean

In the Ryukyu Archipelago (see supplementary Fig. S7), where reproductive populations of coenobitids are mainly distributed in Japan, the larval release seasons of coenobitid crabs extend

from mid-June to late November (Imafuku 2001; Nakasone 2001; Sato and Yoseda 2008; Doi et al. 2016, 2018; Nio et al. 2019; Osaka and Takemura 2019). Hamasaki et al. (2013) suggested that *B. latro* zoeae may inhabit the upper layer in the sea, where spectral light conditions might match the spectral sensitivity of *B. latro* larvae. When we see the profiles of sea surface temperatures (SST) and 50-m-depth temperatures during the larval release seasons of the coenobitid crabs (see supplementary Figs. S8-1 to S8-6 retrieved from the Japan Meteorological Agency), seawater areas with appropriate temperatures (25–31 °C) for the larval survival and development of coenobitids exist broadly around the Ryukyu Archipelago and the Pacific coasts of western Japan.

The Kuroshio Current plays an important role in 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). Our analysis based on the heat summation theory equation describing the relationship between temperature and total zoeal duration of each coenobitid species uncovered the zoeal developmental period at a favourable temperature range between 25 and 31 °C as being between 45 and 25 days in *C. cavipes* and between 25–28 and 13–15 days in the other species (Table 3 and Fig. 5). Emigration behaviour during the sea-to-land transition for megalopae of the six coenobitid species, as observed in the present study, has been examined under laboratory conditions (27–28 °C) (Hamasaki et al. 2014, 2015b). Many megalopae carry empty gastropod shells at 7–14 days of age and first

migrate onto land at 11–22 days of age; then, they moult to the first crab stage after 5–16 days (Hamasaki et al. 2014, 2015b). Therefore, pelagic larvae of coenobitid crabs might disperse broadly throughout the Ryukyu Archipelago and Pacific coasts of western Japan via the Kuroshio Current and its counter currents, after which megalopae migrate onto nearby land. Actually, early juveniles of *C. purpureus* and *C. rugosus* were found on the coasts of the Boso Peninsula (34°58'–35°08'N, 139°46'–140°17'E) (Fig. S7), and only *C. purpureus* successfully overwintered there, because of the strong low-temperature tolerance ability of *C. purpureus* juveniles (Sanda et al. 2019a, 2019b), and grew to maturity (Hamasaki et al. 2019; Sanda et al. 2019b; Inutsuka et al. 2020). Because few (*C. purpureus*) or no (*C. rugosus*) reproductive populations exist on the Pacific coasts of Japan, these juveniles are considered to have originated from the Ryukyu Archipelago (Sanda et al. 2019b; Inutsuka et al. 2020). Sanda et al. (2019b) inferred that among coenobitid crabs, *C. purpureus* and *C. rugosus* are dominant in the northern and southern Ryukyu Archipelago, respectively, and therefore, a large population size might increase the chance of these two species of colonizing the Pacific coast of Japan.

Larvae of coenobitid crabs have the ability to disperse broadly in the ocean, and global warming might increase the chance of successful colonization by more coenobitid species on the Pacific coasts of Japan. Monitoring the northward distributions of early juveniles of coenobitids would assist us in inferring the degree to which global warming is progressing.

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