Vol. 1: 93–107, 2015
doi: 10.3354/sedao00010

SEXUALITY AND EARLY DEVELOPMENT IN AQUATIC ORGANISMS
Sex Early Dev Aquat Org

Published online February 25

Larval growth, development and duration in terrestrial hermit crabs

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ABSTRACT: We investigated patterns of larval growth and development in terrestrial hermit crabs of the family Coenobitidae (genera *Coenobita* and *Birgus*). Larvae of 5 species (*C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro*) were cultured individually at ~28°C, and their moulting, growth and developmental duration were analysed in conjunction with published data for coenobitid species (*C. brevimanus*, *C. cavipes*, *C. clypeatus*, *C. compressus*, *C. purpureus*, *C. rugosus*, *C. scaevola*, *C. variabilis*, and *B. latro*). Coenobitid crabs metamorphosed into megalopae after 2 to 7 zoeal stages, and intraspecific variability in developmental pathways (number of zoeal stages) was observed in 6 out of 10 species. Interspecific variability in body lengths was large at hatching but reduced in megalopae. Linear growth equations ($y = a + bx$) between number of moults (x) and body length (y) in the zoeal stages were determined, parameters a and b representing body length at hatching and mean growth increment at moulting, respectively. The relationship between parameters a and b for the species examined suggested the existence of 4 larval growth and development patterns in coenobitids: (1) initially smaller larvae and smaller growth increments — longer pathway; (2) initially smaller larvae and larger growth increments — shorter pathway; (3) initially larger larvae and smaller growth increments — shorter pathway; and (4) initially largest larvae and smallest growth increments — shortest pathway (abbreviated development). Total zoeal duration increased with decreasing water temperatures and increasing number of zoeal stages and was apparently unrelated to the geographical distribution of coenobitid species.

KEY WORDS: Coconut crab · Land hermit crab · Intraspecific variation · Interspecific variation · Larval duration

INTRODUCTION

Many marine benthic invertebrates develop via complex life cycles comprising embryonic, meroplanktonic larval, and benthic juvenile–adult phases (Anger 2006). In general, pelagic larval duration determines the length of time that larvae are subject to movement by ocean currents, and therefore it is correlated with larval dispersal distance in the sea (Shanks et al. 2003, O'Connor et al. 2007, Shanks 2009). Many benthic decapod crustaceans pass through a planktonic zoeal stage, the duration of which is determined by the number of moults, intermoult period, and body size increment at moulting. They then metamorphose into a megalopa, during which the transition from the plankton to the benthos takes place (Anger 2001, 2006). The number of zoeal instars/stages varies between and among species within evolutionary constraints (Knowlton 1974, Rice 1980, Hines 1986, Anger 2001, 2006). Megalopae

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may actively select a suitable habitat for settlement by detecting abiotic and biotic environmental stimuli such as changes in temperature and salinity, and chemical cues derived from conspecific adults and/or nursery areas (Anger 2001, 2006, Forward et al. 2001). Therefore, the duration of zoeal and megalopal stages should have an effect on population connection and geographical distribution of species through dispersal and recruitment processes.

Terrestrial hermit crabs of the family Coenobitidae comprise 16 species of land hermit crabs of the genus *Coenobita* Latreille, 1829 (McLaughlin et al. 2010), and the coconut crab *Birgus latro* (Linnaeus, 1767). They mainly occur in subtropical and tropical coastal regions (Hartnoll 1988). The coconut crab is the only species in the genus *Birgus*, and is free from gastropod shells except for a juvenile stage that has the shell-carrying habit of its hermit crab ancestors (Reese 1968, Hamasaki et al. 2011, 2014b). It is the largest terrestrial arthropod and has been an important local resource for human consumption (Brown & Fielder 1991). However, coconut crab populations have been severely depleted on most inhabited islands because of overharvesting and habitat loss (Amesbury 1980, Brown & Fielder 1991, Drew et al. 2010). The coconut crab is globally protected, and was first listed as 'Vulnerable' under the IUCN Red List, but was recently categorised as 'Data deficient' in that list — not because the species had recovered but because of the lack of available data (Eldredge 1996, Drew et al. 2010). Land hermit crabs are also the subject of conservation concerns due to their exploitation as ornamental animals (Nakasone 2001, Pavia 2006).

Although coenobitid species are fully terrestrial, females return to the sea to hatch their eggs (Hartnoll 1988, Brown & Fielder 1991, Nakasone 2001), and their larvae develop through planktonic zoeal stages to a megalopa (Nakasone 1988a, Harvey 1992, Brodie & Harvey 2001, Wang et al. 2007, Hamasaki et al. 2009, 2013), similar to marine hermit crab species. After settlement, like marine hermit crabs (Reese 1962, Hazlett & Provenzano 1965), megalopae of terrestrial coenobitid crabs recognise and co-opt gastropod shells before migrating onto land (Reese 1968, Harvey 1992, Brodie 1999, 2002, Hamasaki et al. 2011). Therefore, information on larval growth, development and duration before metamorphosis into the megalopae is essential for a better understanding of the geographical distribution and population connection of coenobitid species, which in turn have implications for conservation of populations.

The number of zoeal stages, zoeal duration, and body length at zoeal and megalopal stages based on laboratory rearing have been reported for 9 coenobitid species: *C. brevimanus* Dana, 1852 (Hamasaki et al. 2014a), *C. cavipes* Stimpson, 1858 (Shokita & Yamashiro 1986, Nakasone 1988a), *C. clypeatus* (Fabricius, 1787) (Provenzano 1962), *C. compressus* H. Milne-Edwards, 1836 (Brodie & Harvey 2001), *C. purpureus* Stimpson, 1858 (Nakasone 1988a), *C. rugosus* H. Milne-Edwards, 1837 (Shokita & Yamashiro 1986, Nakasone 1988a), *C. scaevola* (Forskål, 1775) (Al-Aidaroos & Williamson 1989), *C. variabilis* McCulloch, 1909 (Harvey 1992), and *B. latro* (Reese & Kinzie 1968, Wang et al. 2007, Hamasaki et al. 2009, Sugizaki et al. 2010). These studies demonstrated intra- and interspecific variations in the number of zoeal stages, i.e. the developmental pathway to reach the megalopa stage. However, use of an individual culture method whereby the moulting history of individual larvae reared in separate compartments is followed (Brodie & Harvey 2001) has been applied for 5 species only: *C. brevimanus* (Hamasaki et al. 2014a), *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989) and *C. variabilis* (Harvey 1992). Reese & Kinzie (1968) also employed the individual culture method for larval rearing of *B. latro*, but their data were based mainly on group culture, which cannot follow the moulting history of individual larvae.

Wang et al. (2007) compared the larval development of 8 coenobitid species in terms of ecological adaptation, taking adult habitats, body length of the glaucothoe (=megalopae), and zoeal life span (number of zoeal stages) into consideration. They categorised 4 development types: mangrove adaptation, larger glaucothoe adaptation, smaller glaucothoe adaptation, and hypersaline adaptation. However, the interspecific variation in the body length at hatching was not taken into account, and the relationship between larval body length and number of zoeal stages was not analysed thoroughly.

Our objective with this study was to investigate patterns of larval growth and development in coenobitid species. Larvae of 5 species (*C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens* Heller, 1862, and *Birgus latro*), whose ovigerous females can be found and collected in subtropical Japan, were cultured individually, and their moulting, growth and developmental duration were analysed in conjunction with published data for coenobitid species (*C. brevimanus*, *C. cavipes*, *C. clypeatus*, *C. compressus*, *C. purpureus*, *C. rugosus*, *C. scaevola*, *C. variabilis*, and *B. latro*).

MATERIALS AND METHODS

Larval source

All species belonging to the genus *Coenobita* in Japan are recognised collectively as a Natural Monument, to promote their conservation. Therefore, *Coenobita* species were collected and cultured with the permission of the Agency for Cultural Affairs, Ministry of Education, Culture, Sports, Science and Technology of Japan. In addition, the coconut crab is listed as 'Vulnerable' in the Red Data Book by the Ministry of the Environment of Japan. Therefore, after the end of the culture experiments, collected crabs were returned to their natural habitats.

Culture experiments were conducted in the laboratory at the Tokyo University of Marine Science and Technology during the reproductive season of each species from 2009 to 2011. Ovigerous females of *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *Birgus latro* were captured by hand during late June to early July on Hatoma Island (24° 28' N, 123° 49' E), Ishigaki Island (24° 23–31' N, 124° 07–18' E), and/or Miyako Island (24° 43–50' N, 125° 15–21' E), Okinawa Prefecture, southern Japan. They were transported to the laboratory by air and maintained in tanks equipped with land space and a sea area (artificial seawater, ~34‰ salinity; Sealife, Marinetech) until hatching occurred at ~28°C in air according to the method of Hamasaki et al. (2009) and Hamasaki (2011). Females hatched their eggs into the seawater (~28°C) in tanks at night and the newly hatched larvae (0 d old) were collected from the tank using a 1 l beaker in the early morning.

Larval culture

The larvae hatched from 2 females, designated as Broods 1 and 2, were cultured for each species. Two groups, each including 30 newly hatched larvae (total 60) randomly selected from each brood, were prepared. The first group of larvae was used for body length measurements, and the second group of larvae for examining survival and moulting history. Larvae were housed individually in the wells of 10 six-well cell culture plates (10 ml seawater in each well). The culture medium and conditions, artificial seawater controlled at ~28°C and ~34‰ salinity and a photoperiod in the culture room of 13–14 h light:11–10 h dark, were similar to the natural conditions during the reproductive season. Larvae were fed *Artemia* sp. and the rotifer *Brachionus plicatilis* species complex. *Artemia* (Utah strain) aged 2 d were enriched with a commercial material containing n-3 highly unsaturated fatty acids (SCP, Chlorella Industry) for 4 h and then fed to the larvae at 2 individuals ml^{-1}. The rotifer *B. plicatilis* species complex, cultured with the phytoplankton *Chlorella vulgaris* containing n-3 highly unsaturated fatty acids in its cells (Super Chlorella V12, Chlorella Industry), was also given to the crab larvae at 40 individuals ml^{-1}. The larvae were transferred to clean culture wells with fresh seawater and food daily, and each larval moulting was determined by the presence of an exuvia. No larvae fed on their exuviae.

The larvae of each zoeal and megalopal stage (2–5 specimens, depending on the survivors from each brood of each species) were randomly sampled from the first culture group, and fixed with 5% neutral formalin for 1 d and then preserved in 70% ethanol. In *C. cavipes*, megalopae were also sampled from the second culture group because of the limited number of larvae in the first group. The specimens of final-stage zoeae and megalopae in the minor developmental pathway were not sampled for some species and/or broods because of the limited number of final stage zoeae or use of megalopae for other culture studies. Body length measurements of the specimens were made using a microscope equipped with a digital camera and image analysing system (Nikon Digital Sight and NIS-Elements software) as previously described for larvae of coenobitid crabs (e.g. see Wang et al. 2007) (see Fig. S1 in the Supplement for body length measurements; www.int-res.com/articles/suppl/s001p093_supp.pdf). Total length (TL) was measured from the tip of the rostrum to the midpoint of the telson excluding the telson processes, and carapace length (CL) was measured from the tip of the rostrum to the posteromedial margin of the carapace.

Data sources

Larval growth and developmental patterns were compared among 5 species cultured in this study using moulting and growth data including developmental pathway (number of zoeal stages before metamorphosing into the megalopal stage), body lengths (TL and CL) and intermoult period (days) of each stage, and total zoeal duration (number of days required from hatching to moulting to the megalopa). The same data from 2 broods of *C. brevimanus* whose larvae were reared using the same culture protocol by the present authors (Hamasaki et al. 2014a) were also

included in our analysis. In addition, previously published larval moulting and growth data including developmental pathway, body lengths (TL and CL), intermoult period, and total zoeal duration from individually cultured larvae of 4 species — *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), and *C. variabilis* (Harvey 1992) — were also included in the analysis. Furthermore, larval developmental pathways from individually cultured larvae of *B. latro* (Reese & Kinzie 1968) and total zoeal duration with information of larval rearing temperatures from group-cultured larvae of *C. cavipes* (Nakasone 1988a), *C. purpureus* (Nakasone 1988a), *C. rugosus* (Shokita & Yamashiro 1986, Nakasone 1988a), and *B. latro* (Reese & Kinzie 1968, Wang et al. 2007, Hamasaki et al. 2009) were used for interspecific analysis. Al-Aidaroos & Williamson (1989) reported that the total zoeal duration of *C. scaevola* was 47 d, but the summation of the intermoult period (days) of each zoeal stage listed in their Table 1 was 67 d. In the present study, therefore, we adopted 67 d for the total zoeal duration of *C. scaevola*. The data from the literature were mean values (with standard deviations) or median values in the range. In the coenobitid crabs, intra- and interspecific comparisons of larval growth based on body length metrics could be made because larvae keep very similar body shapes during zoeal stages in each species and body shapes of zoeae and megalopae are very similar among species (Provenzano 1962, Reese & Kinzie 1968, Shokita & Yamashiro 1986, Nakasone 1988a, Al-Aidaroos & Williamson 1989, Harvey 1992, Brodie & Harvey 2001, Hamasaki et al. 2014a). Larval rearing conditions such as water temperature, salinity, food, initial stocking number of larvae, and water volume of culture containers are summarised for all species in Table S1 in the Supplement.

Statistical analysis

All statistical analyses were performed with R language (R3.1.0; R Development Core Team 2014) with a 5% significance level. We applied a generalised linear mixed-effects model (GLMM) (Everitt 2005, Everitt & Hothorn 2009, Zuur et al. 2009) with the Gaussian family (identical link) distribution to examine the differences of body length represented by TL among 6 species reared in our laboratory. In this analysis, species was the categorical explanatory variable and brood number of each species was included as a random intercept effect. Similarly, the GLMM with the Poisson family (logarithmic link) distribution was performed to evaluate the differences in total zoeal duration among 6 species. The statistical significance of the explanatory variable was evaluated with a Wald χ^2-test (Poisson family) or a Wald *F*-test with Kenward–Roger degrees of freedom (Kenward & Roger 1997, Halekoh & Højsgaard 2013) (Gaussian family) using the *Anova* function (type II) implemented in the car package (Fox & Weisberg 2011), and the *glmer* (Poisson family) or *lmer* (Gaussian family) function in the lme4 package (Bates et al. 2014). The total zoeal duration between different developmental pathways in *C. cavipes* Brood 1 and in *C. purpureus* Brood 2 were compared with a likelihood ratio test using the *Anova* function and the *glm* function for a generalised liner model with the Poisson family. This test was not performed for other species/broods with intraspecific variations in developmental pathway because there was only one sample in the minor pathway. The TL of megalopae between different developmental pathways in *C. cavipes* Brood 1 was compared with the *lm* function and an *F*-test using the *Anova* function.

The relationship between 2 variables such as body lengths at hatching and the megalopal stage, and larval body lengths and number of zoeal stages was evaluated using a Pearson product-moment correlation coefficient (r) with a *t*-test.

The linear growth equation, $y = a + bx$, was applied to express the relationship between number of moults (x) and body lengths (TL and CL) (y) in each brood of 6 species — *C. brevimanus* (Hamasaki et al 2014a), and *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro* (present study) — reared in our laboratory, and in individually cultured larvae of 4 species from other studies: *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), and *C. Variabilis* (Harvey 1992) (total 10 species). The parameters a and b were estimated and evaluated using the *lm* function. In this growth model, the value of the explanatory variable (number of moults) ranged from 0 to 6 depending on the species, and parameters a and b represent the body length at hatching and body length increment at moulting, respectively. In the species with intraspecific variations in the developmental pathway, the growth equation was applied to the major developmental pathway in *C. cavipes* Brood 2, *C. purpureus* Broods 1 and 2, and *C. rugosus* Broods 1 and 2 reared in our laboratory, and *C. clypeatus* (Provenzano 1962) and *C. compressus* (Brodie & Harvey 2001) from other studies, and it was estimated using the combined

data from both pathways in *C. cavipes* Brood 1 reared in our laboratory. The body lengths of megalopae were not included in the analyses because megalopae have relatively shorter rostrums than zoeae and the linearity of the growth equation is therefore not supported over the entire larval period. Hierarchical cluster analysis was performed to evaluate patterns in the relationship between initial body length (parameter *a*) and growth increment (parameter *b*) in 10 coenobitid species. The analyses were conducted using the *hclust* function with 8 clustering methods (complete linkage, single linkage, group average, centroid, median, Ward [Ward.D, Ward.D2], and McQuitty methods), based on the Euclidean distance calculated from the standardised scores of the respective parameter estimates for TL and CL.

It is well known that temperature significantly affects larval developmental duration in marine organisms, including decapod crustaceans (Anger 2001, O'Connor et al. 2007). In the present study, and in a study on *C. brevimanus* (Hamasaki et al 2014a), larvae were cultured at ~28°C, whereas in other studies larval rearing temperatures varied from 21 to 32°C (Table S1). Therefore, the relationship between water temperature (T) and total zoeal duration (D) was fitted with the following equation in 10 coenobitid species: $D = K/(T - \alpha)$. This equation, known as Réaumur's Law, is part of the theory of heat summation; the parameters K and α are the so-called 'thermal constant' and 'threshold temperature' for development, respectively, as previously estimated for *B. latro* (Hamasaki et al. 2009). The thermal constant (degree days) is the summation of the effective temperature for development (>threshold temperature) up to a selected biological end point. In this analysis, total zoeal duration tended to increase with an increase in the number of zoeal stages at identical temperatures (see 'Results'). The thermal constant K was therefore expressed as the following function: $K = \beta + \gamma S$, where S is the number of zoeal stages, and β and γ are parameters. Thus, the relationship between temperature and the total zoeal duration was expressed as: $D = (\beta + \gamma S)/(T - \alpha)$. The parameters α, β and γ were estimated using a non-linear ordinary least squares method and evaluated with a *t*-test.

RESULTS

Larval developmental pathway

Larval survival rates to metamorphosis to megalopae were over 80% in the species cultured in our laboratory excluding *Birgus latro* (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/s001p093_supp.pdf for changes in the number of larvae according to larval stage in each species).

Intraspecific variations in the developmental pathway were not found in *Coenobita brevimanus*, *C. violascens*, or *B. latro*, all of which had 4 zoeal stages (Fig. 1A), although one larva of *B. latro* moulted to a stage 5 zoea that died without further moulting (Fig. S2). Larvae of *C. purpureus* and *C. rugosus* moulted to the megalopal stage through stage 4 or 5 zoeae with the major developmental

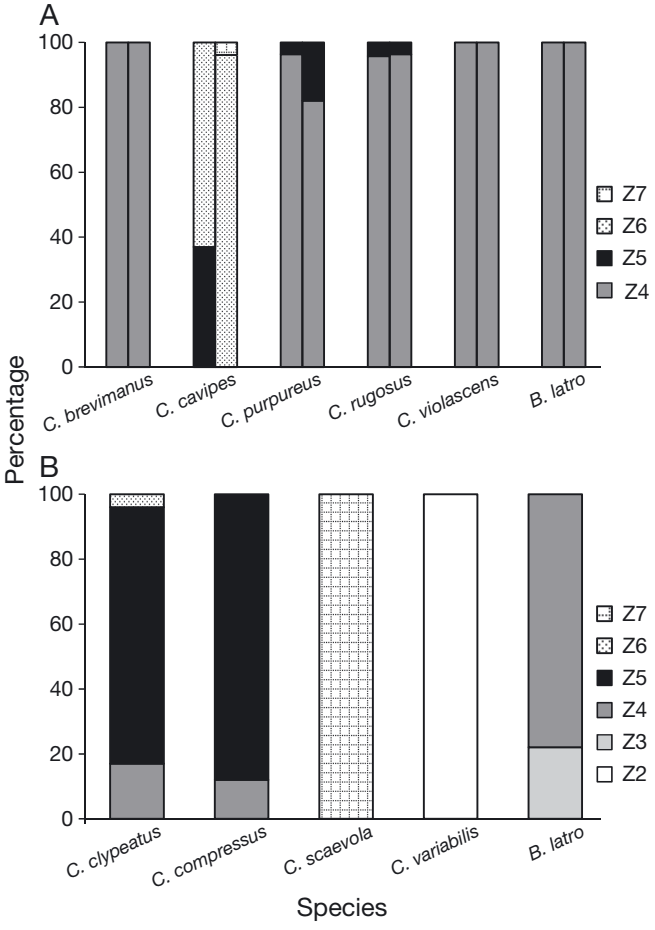

Fig. 1. Composition of larval developmental pathways in *Coenobita* spp. and *Birgus latro*. Data are shown for (A) individually cultured larvae from 2 broods of 6 species, *C. brevimanus* (Hamasaki et al. 2014a), and *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro* (present study), reared in our laboratory (left and right bars are from Broods 1 and 2, respectively), and (B) individually cultured larvae of 5 species, *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), *C. variabilis* (Harvey 1992), and *B. latro* (Reese & Kinzie 1968). Larval developmental pathway: number of zoeal stages required to metamorphose into the megalopal stage (Z2–Z7: second to seventh zoeal stages)

pathway through the stage 4 zoeae. *C. cavipes* had longer developmental pathways with variations in the different broods: 5 or 6 zoeal stages (mostly 6) in Brood 1, and 6 or 7 zoeal stages (mostly 6) in Brood 2.

The numbers of zoeal stages of other *Coenobita* species based on individual culture results were as follows (Fig. 1B): *C. clypeatus*, 4, 5 or 6 stages (mostly 5) (Provenzano 1962); *C. compressus*, 4 or 5 stages (mostly 5) (Brodie & Harvey 2001); *C. scaevola*, 7 stages (Al-Aidaroos & Williamson 1989); *C. variabilis*, 2 stages (Harvey 1992); and *B. latro*, 3 or 4 stages (mostly 4) (Reese & Kinzie 1968). Thus, intraspecific variability in developmental pathways was observed in individually cultured larvae of 6 out of 10 coenobitid species.

Larval growth and development

The TL of the stage 1 zoeae was significantly different among 6 species cultured in our laboratory (F = 22.62, df = 5, 6.0, p = 0.0007914; Fig. 2A) (see Table S2 in the Supplement for all body length data). Mean or median TL of the stage 1 zoeae is also shown for 4 described coenobitid species in Fig. 2B (see Table S3 in the Supplement for all body length data). *Coenobita variabilis*, with abbreviated, lecithotrophic larval development (2 zoeal stages) (Harvey 1992), was much larger at hatching than the other species. Thus, interspecific variation of TL at hatching was large and the coefficient of variation (CV) was calculated at 28% using the average (or median) values of the respective species.

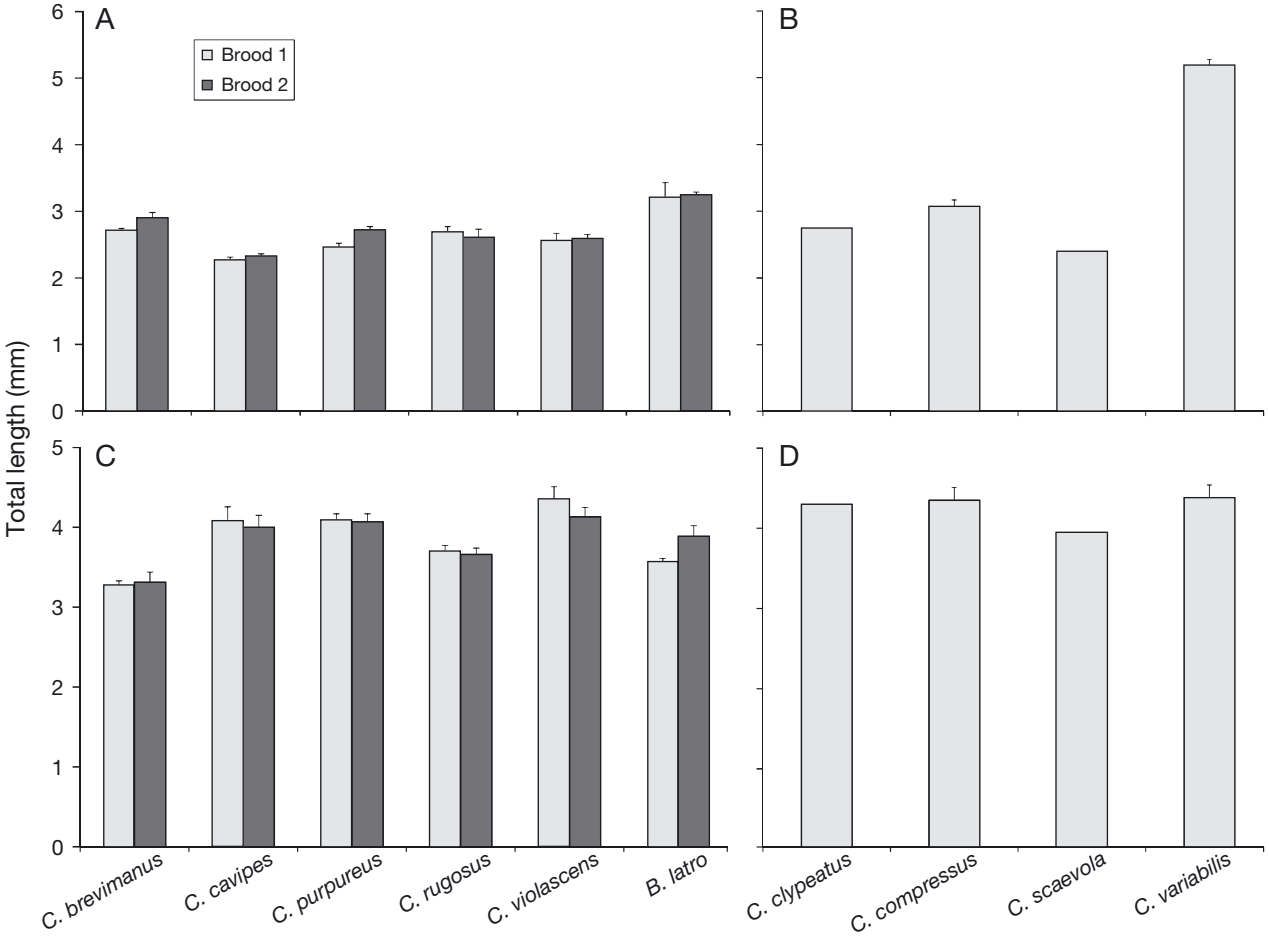

Fig. 2. Total length of the (A,B) stage 1 zoeae and (C,D) megalopae in *Coenobita* spp. and *Birgus latro*. Total length was measured from the tip of the rostrum to the midpoint of the telson, excluding the telson processes. (A,C) Mean values are shown for individually cultured larvae from 2 broods of 6 species, *C. brevimanus* (Hamasaki et al. 2014a), and *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro* (present study), reared in our laboratory. (B,D) Mean values or median values in the range are shown for individually cultured larvae of 4 species, *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), and *C. variabilis* (Harvey 1992). Vertical bars indicate the standard deviations. See Fig. S1 in the Supplement for body length dimensions, and Tables S2 and S3 in the Supplement for data on body length measurements of each species (www.int-res.com/articles/suppl/s001p093_supp.pdf)

The TL of the megalopae between the different developmental pathways was not significantly different in *C. cavipes* Brood 1 (F = 0.6531, df = 1, 8, p = 0.6531). The megalopal TL was, however, significantly different among the 6 species (F = 17.79, df = 5, 6.0, p = 0.001552; Fig. 2C). However, the trend of differences in the initial TL of the species (Fig. 2A,B) was not found at the megalopal stage (Fig. 2C,D), and the interspecific variation in the TL was largely reduced as shown by the lower CV value (9%). Therefore, a significant relationship between the initial TL and megalopal TL was not found (Table 1). This trend was also observed even after excluding *C. variabilis*, with abbreviated larval development, from the analysis (Table 1).

The number of zoeal stages in the major developmental pathway was negatively correlated with TL at hatching but not with megalopal TL (Table 1). This result may be biased by including *C. variabilis*, which has a much larger size at hatching and 2 zoeal stages, in the analyses. However, a similar trend was found in the relationship between the number of zoeal stages and larval TL even after excluding *C. variabilis* from the analyses (Table 1). Therefore, initial larval body length appears to determine the developmental pathway in coenobitid species, and initially smaller/larger larvae require more/fewer moults to reach a given body length at the megalopal stage.

The linear growth equations expressing the relationship between number of moults and body length (TL and CL) were a good fit for the zoeal stages of 10 species (Fig. 3 and see Tables S4 & S5 in the Supplement for parameter estimates and statistics). Parameter *a* represents the initial body length of larvae, as illustrated by the same trend in the interspecific variability between the values of initial TL (Fig. 2A,B) and estimates of parameter *a* for TL (Fig. 4A,B). Parameter *b* represents the mean growth increment at moulting and tended to be lowest in *C. variabilis*, followed by *C. scaevola* and *C. cavipes*, and larger in *C. purpureus*, *C. rugosus*, and *C. violascens* (Fig. 4C,D).

The linear growth equations include information on 3 important early life-history traits: initial body length, growth increment at moulting, and number of moults to the megalopal stage (developmental pathway). Initial body length tended to be negatively correlated with the number of zoeal stages before moulting to the megalopal stage as mentioned above. Here, to see the relationship between the initial body length and growth increment in larvae of 10 coenobitid species, estimates of parameter *a* are plotted against those of parameter *b* for TL and CL in Fig. 5. Based on these parameter estimates, 7 out of 8 clustering methods resulted in similar dendrograms that categorise 4 groups (2 representative dendrograms are shown in Fig. 6; see Fig. S3 in the Supplement for other dendrograms). Characteristics of these 4 groups are summarised as follows: (1) species with initially smaller larvae and smaller growth increments, showing longer developmental pathways (*C. cavipes*, mostly 6 stages; *C. scaevola*, 7); (2) species with initially smaller larvae and larger growth increments, showing shorter developmental pathways (*C. purpureus*, mostly 4; *C. rugosus*, mostly 4; *C. violascens*, 4); (3) species with initially larger larvae and smaller growth increments, showing shorter developmental pathways (*C. brevimanus*, 4; *C. clypeatus*, mostly 5; *C. compressus*, mostly 5; *B. latro*, mostly 4); and (4) species with initially largest larvae and smallest growth increments, showing the shortest developmental pathway (abbreviated development) (*C. variabilis*, 2).

Table 1. Pearson product-moment correlation coefficient (r) of the relationship among total length (TL) of the stage 1 zoeae, TL of megalopae, and number of zoeal stages in the major developmental pathway in 10 coenobitid species:, *Coenobita brevimanus*, *C. cavipes*, *C. clypeatus*, *C. compressus*, *C. purpureus*, *C. rugosus*, *C. scaevola*, *C. variabilis*, *C. violascens*, and *Birgus latro*

Variables	Species analysed	*r*	df	*t*	p
Initial zoeal TL and megalopal TL	All species	0.199	15	0.758	0.4609
	Excluding *C. variabilis*	–0.246	14	–0.914	0.3771
Initial zoeal TL and number of zoeal stages	All species	–0.689	15	–3.557	0.0031
	Excluding *C. variabilis*	–0.510	14	–2.136	0.0523
Megalopal TL and number of zoeal stages	All species	0.049	15	0.183	0.8572
	Excluding *C. variabilis*	0.300	14	1.132	0.2781

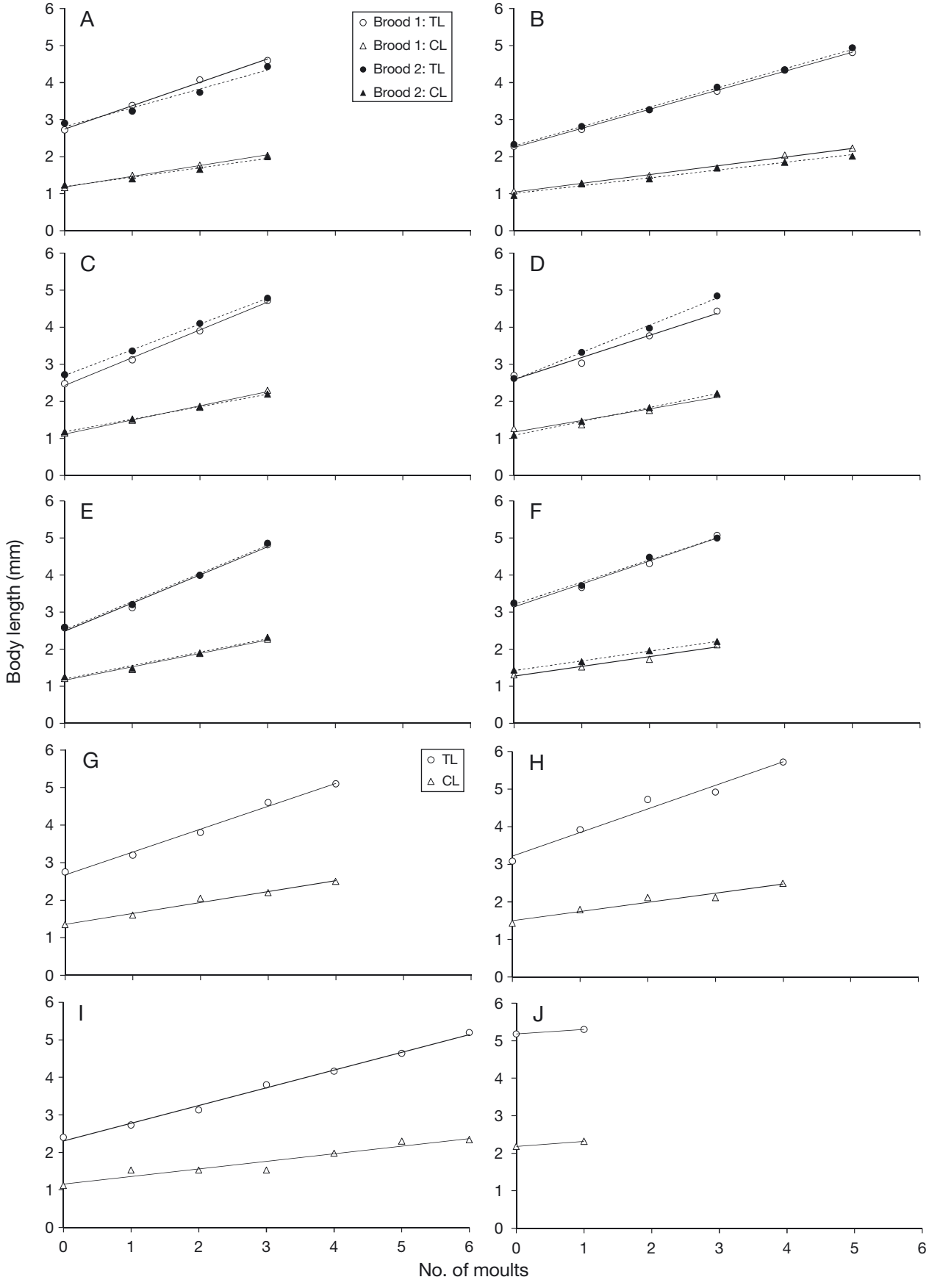
A
B
C
D
E
F
G
H
I
J
Brood 1: TL
Brood 1: CL
Brood 2: TL
Brood 2: CL
TL
CL
Body length (mm)
No. of moults

Fig. 3. Growth expressed by the relationship between number of moults and body length in *Coenobita* spp. and *Birgus latro*. Mean values of body lengths (total length [TL] and carapace length [CL]) are shown for individually cultured larvae of 2 broods of 6 species, (A) *C. brevimanus* (Hamasaki et al. 2014a), and (B) *C. cavipes*, (C) *C. purpureus*, (D) *C. rugosus*, (E) *C. violascens*, and (F) *B. latro* (present study), reared in our laboratory, and mean values or median values in the range of TL and CL for individually cultured larvae of 4 species, (G) *C. clypeatus* (Provenzano 1962), (H) *C. compressus* (Brodie & Harvey 2001), (I) *C. scaevola* (Al-Aidaroos & Williamson 1989), and (J) *C. variabilis* (Harvey 1992). TL was measured from the tip of the rostrum to the midpoint of the telson, excluding the telson processes. CL was measured from the tip of the rostrum to the posteromedial margin of the carapace. Solid and dotted lines in A–F correspond to Broods 1 and 2, respectively. See Fig. S1 in the Supplement for body length dimensions, and Tables S4 & S5 in the Supplement for parameter estimates of the linear growth equations (www.int-res.com/articles/suppl/s001p093_supp.pdf)

Larval duration

The intermoult periods of larvae before the final zoeal stage were 3–5 d on average, and they increased to 5–9 d in the final stage in 6 species (Fig. 7; see Table S6 in the Supplement for larval duration). This trend, i.e. increasing the intermoult period in the final zoeal stage, was also observed in *C. compressus* and *C. variabilis* (see Table S7 in the Supplement). Average total zoeal duration was the same in the different developmental pathways in *C. cavipes* Brood 1, but tended to be slightly longer in the longer pathway in *C. cavipes* Brood 2, *C. purpureus* Broods 1 and 2, and *C. rugosus* Broods 1 and 2 (Fig. 7). A significant difference was not detected between the 2 pathways in the species/broods for

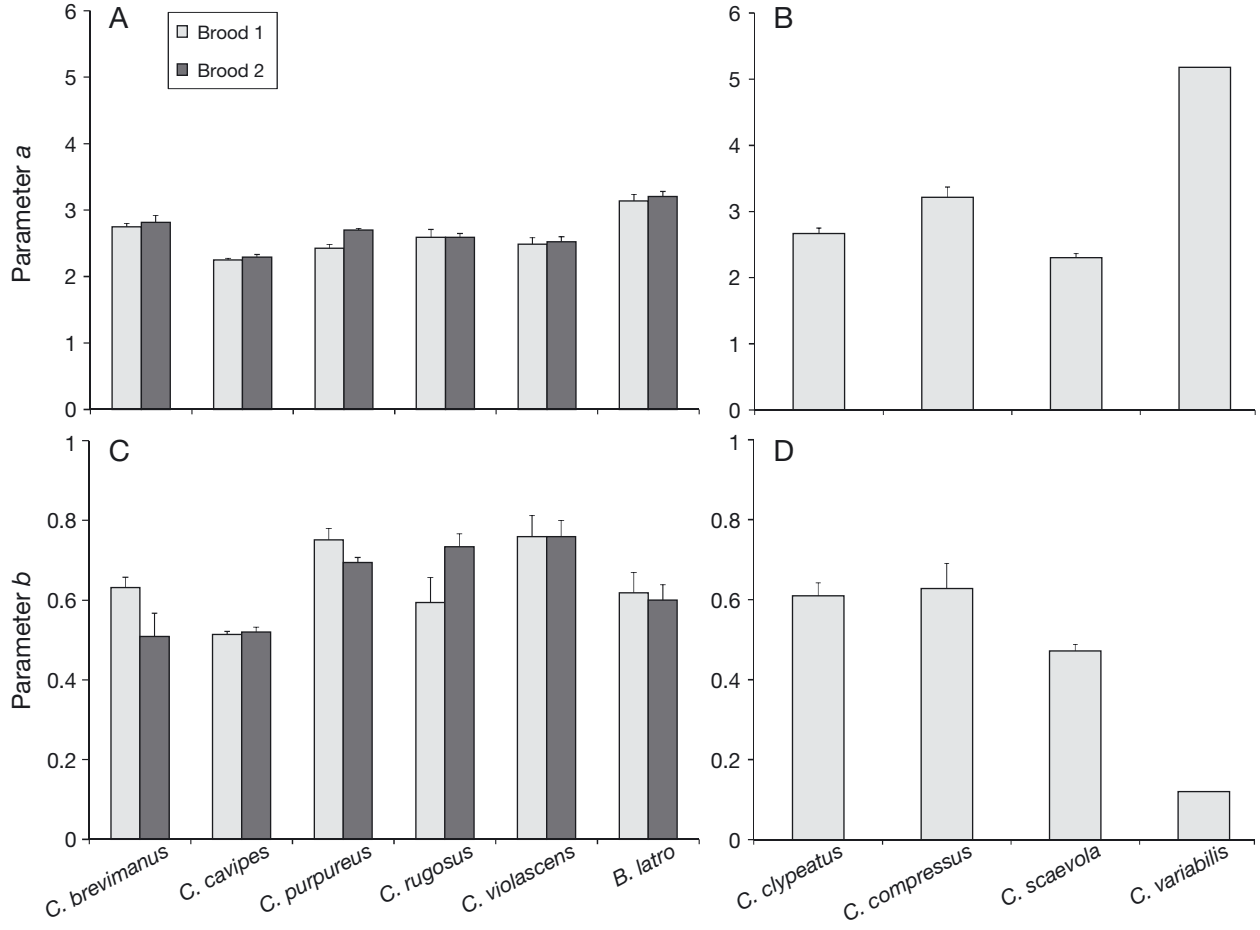

Fig. 4. Estimates of (A,B) parameter *a* and (C,D) parameter *b* in the linear growth equations for the relationship between number of moults and body length (total length) in *Coenobita* spp. and *Birgus latro*. Estimates are shown for (A,C) individually cultured larvae from 2 broods of 6 species, *C. brevimanus* (Hamasaki et al. 2014a), and *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro* (present study), reared in our laboratory, and (B,D) individually cultured larvae of 4 species, *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), and *C. variabilis* (Harvey 1992). Vertical bars indicate the standard errors. See Tables S4 & S5 in the Supplement for parameter estimates and statistics for each body length measurement (www.int-res.com/articles/suppl/s001p093_supp.pdf)

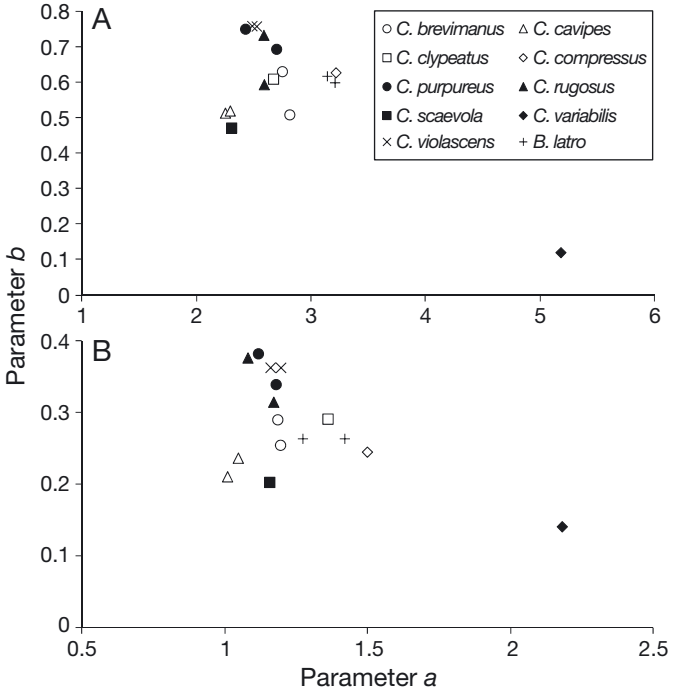

Fig. 5. Relationship between the estimates of parameters *a* and *b* in linear growth equations for *Coenobita* spp. and *Birgus latro*. Diagrams are shown for (A) total length and (B) carapace length. See Tables S4 & S5 in the Supplement for parameter estimates of each species (www.int-res.com/articles/suppl/s001p093_supp.pdf)

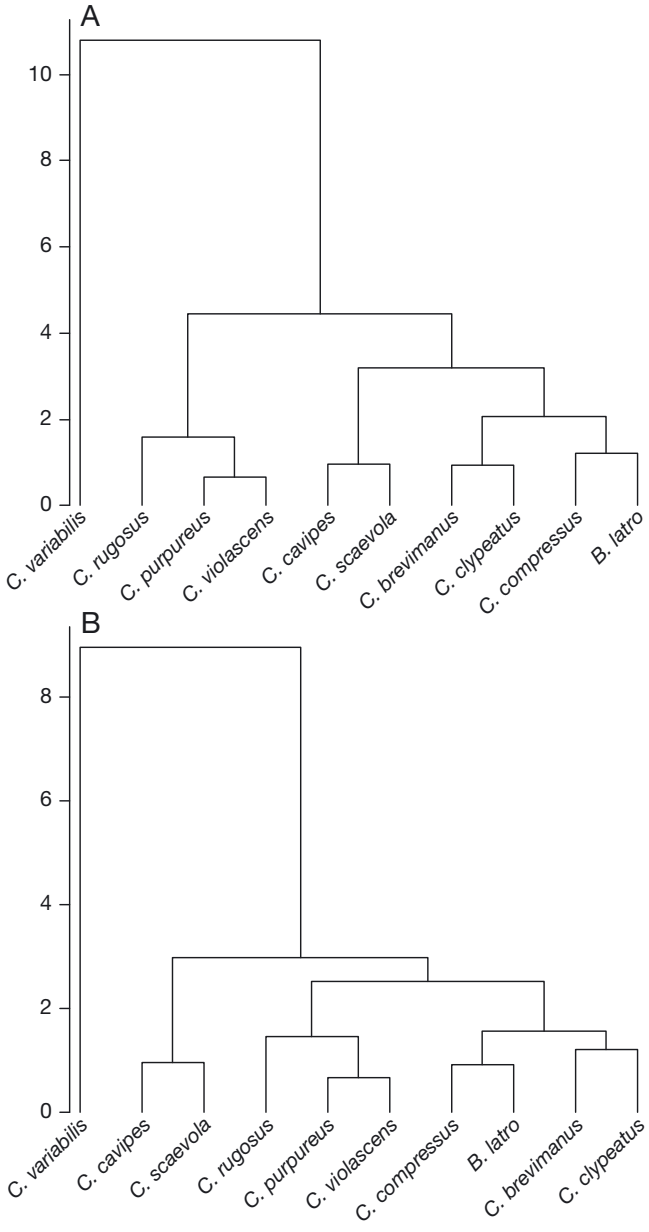

Fig. 6. Dendrograms of 10 coenobitid species (*Coenobita* spp. and *Birgus latro*) as defined by cluster analysis with 2 clustering methods, (A) complete linkage and (B) McQuitty, based on the Euclidean distance calculated from the standardised scores of respective parameter estimates in the linear growth equations for total length (TL) and carapace length (CL). See Fig. S3 in the Supplement for dendrograms based on 6 other clustering methods (www.int-res.com/articles/suppl/s001p093_supp.pdf)

which the statistical test was able to be performed (*C. cavipes* Brood 1: $\chi^2 = 0.00013$, df = 1, p = 0.9909; *C. purpureus* Brood 2: $\chi^2 = 1.6005$, df = 1, p = 0.2058).

Total zoeal duration was significantly different among the 6 species ($\chi^2 = 294.8$, df = 5, $p < 0.0001$); it was longer in *C. cavipes* (with more zoeal stages) compared with the other species (Fig. 7). In 10 coenobitid species, total zoeal duration tended to decrease with increasing temperature, and it appeared to vary depending on the developmental pathways (Fig. 8): longer duration in *C. scaevola* with 7 zoeal stages at 25°C and shorter duration in *C. variabilis* with 2 zoeal stages at 25°C and 30°C. Parameters of the heat summation theory equation, $D = (\beta + \gamma S)/(T - \alpha)$, between temperature ($T$) and total zoeal duration (D) including the number of zoeal stages (S) as the explanatory variable, were estimated as shown in Table 2. Parameters α and γ were significantly different from zero, while β was not significant.

DISCUSSION

We successfully conducted the individual culture of larvae at 28°C for 6 coenobitid species including *Coenobita brevimanus* (Hamasaki et al. 2014a). Furthermore, the larval culture from hatching to the megalopa stage was achieved for the first time for *C. violascens*. Our results and those of previous studies demonstrate intra- and interspecific variation in the larval developmental pathways, with variable larval

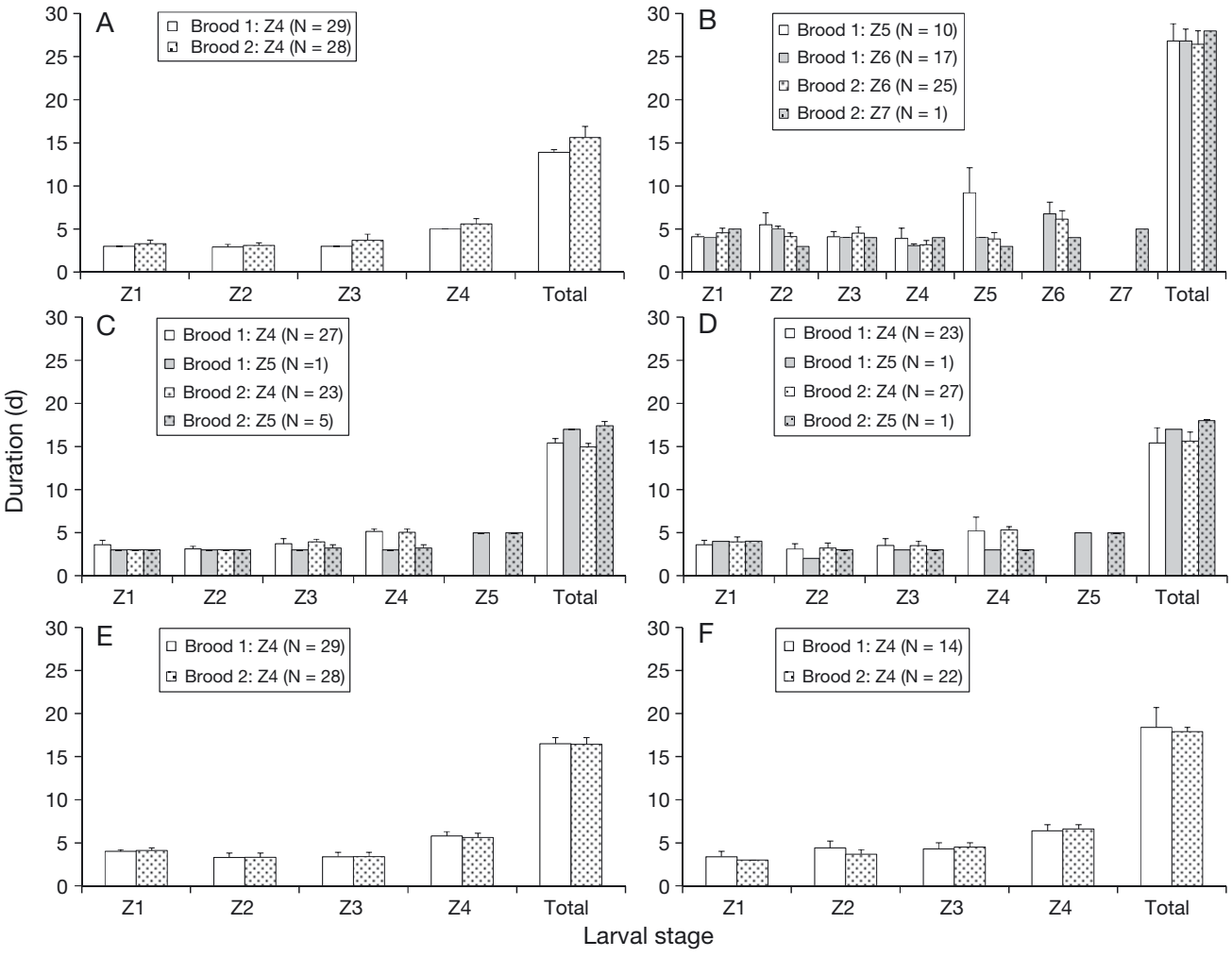

Fig. 7. Larval duration in each zoeal stage and total zoeal duration from hatching to moulting to the megalopal stage in *Coenobita* spp. and *Birgus latro*. Mean values are shown for respective developmental pathways in individually cultured larvae from 2 broods of 6 species: (A) *C. brevimanus* (Hamasaki et al. 2014a), and (B) *C. cavipes*, (C) *C. purpureus*, (D) *C. rugosus*, (E) *C. violascens*, and (F) *B. latro* (present study), reared in our laboratory. Vertical bars indicate the standard deviations. Z1–Z7: first to seventh zoeal stages. See Table S6 in the Supplement for data on the larval duration of each species (www.int-res.com/articles/suppl/s001p093_supp.pdf)

duration depending on water temperature and number of zoeal stages.

Intraspecific variability in larval growth and development

Laboratory and field studies have reported intraspecific variability in larval developmental pathways of 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, temperatures, and limited nutritional conditions (Anger 2001, Zeng et al. 2004). Our data and that of previously published studies revealed that intraspecific variability in developmental pathways has been observed in individually cultured larvae of 6 out of 10 coenobitid species. Our results also demonstrated that 3 species previously thought to exhibit a constant number of zoeal stages (*C. cavipes*, *C. purpureus*, and *C. rugosus*) (Brodie & Harvey 2001, Wang et al. 2007) in fact exhibited variability in the number of zoeal stages. Brodie & Harvey (2001) suspected that the reported lack of variability in the number of zoeal stages in these species might be an artefact of the group culture of larvae.

Knowlton (1974) hypothesised that food energy is utilised for maintenance activities at the expense of the moulting process, which in turn has priority over

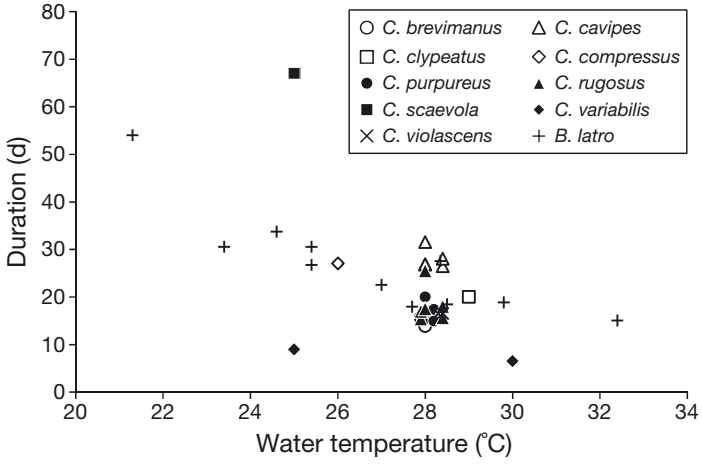

Fig. 8. Relationship between water temperature and total zoeal duration from hatching to moulting to the megalopal stage in *Coenobita* spp. and *Birgus latro*. Data sources are as follows: individually cultured larvae from 2 broods of 6 species, *C. brevimanus* (Hamasaki et al. 2014a), and *C. cavipes*, *C. purpureus*, *C. rugosus*, *C. violascens*, and *B. latro* (present study), reared in our laboratory; individually cultured larvae of 4 species, *C. clypeatus* (Provenzano 1962), *C. compressus* (Brodie & Harvey 2001), *C. scaevola* (Al-Aidaroos & Williamson 1989), and *C. variabilis* (Harvey 1992); and group-cultured larvae of *C. cavipes* (Nakasone 1988a), *C. purpureus* (Nakasone 1988a), *C. rugosus* (Shokita & Yamashiro 1986, Nakasone 1988a), and *B. latro* (Reese & Kinzie 1968, Wang et al. 2007, Hamasaki et al. 2009)

growth and morphogenesis, resulting in a longer developmental pathway under environmental stress. Anger (2001) stated that the optimal temperature range for rearing larvae of subtropical and tropical crab species is usually >25°C, whereas temperatures <20°C increase larval mortality. Hamasaki et al. (2009) conducted group culture of *Birgus latro* larvae at 6 different temperatures (~19–32°C) and found that stage 5 zoeae that died without further moulting occurred in groups with lower survival rates at temperatures lower than 25°C. In the present study, larval mortality rate tended to be high in *B. latro* compared with other species, and a stage 5 zoea that died without further moulting occurred in Brood 1.

Table 2. Parameter estimates with standard errors (SE) of the heat summation theory equation, $D = (\beta + \gamma S)/(T - \alpha)$, between temperature ($T$) and total zoeal duration (D), including the number of zoeal stages (S) in 10 coenobitid species. The number of data points for estimating parameters was 36

Parameter	Estimate	SE	t	p
α	18.01	0.58	31.316	<0.0001
β	–43.01	35.53	–1.211	0.2350
γ	55.27	8.22	6.724	<0.0001

Accordingly, it is suggested that the intraspecific variation in the larval developmental pathways of subtropical and tropical coenobitid crabs might be attributed to environmental stress (e.g. lower water temperatures), different nutritional conditions of individual larvae under identical rearing conditions, and/or maternal factors.

Larval culture studies under the various environmental and nutritional conditions are still needed to evaluate the flexibility in the developmental pathways of species for which variability in developmental pathways has not been reported: *C. brevimanus*, *C. scaevola*, and *C. violascens*—excluding *C. variabilis*, which exhibits abbreviated larval development. Furthermore, we could not evaluate the intraspecific growth variations in individually cultured larvae of coenobitid species because we sampled larvae at each zoeal stage and the subsequent developmental pathway of these larvae could therefore not be known. Thus, our larval growth data were derived from the major developmental pathways. To understand the variability in relationships between growth and developmental pathways at the individual larva level, another approach to obtaining the measurements, e.g. measuring exuviae after moulting, would be necessary in future studies.

Interspecific variability in larval growth and development

Larger maternal investment in individual larvae facilitates larval development of the estuarine crab *Neohelice* (*Chasmagnathus*) *granulata* and the caridean shrimp *Palaemonetes varians* through shorter pathways (Giménez & Torres 2002, Giménez & Anger 2003, Giménez et al. 2004, Oliphant & Thatje 2013, Oliphant et al. 2013). Variability in larval development patterns mediated by body length variation at hatching was observed at the interspecific level in the coenobitid species; initially, smaller larvae of *C. cavipes* and *C. scaevola* had longer developmental pathways, whereas the largest larvae of *C. variabilis* underwent abbreviated larval development.

Wang et al. (2007) categorised 4 larval development types in coenobitids based on adult habitats, body length of the glaucothoe (=megalopae), and number of zoeal stages: (1) mangrove adaptation (*C. variabilis*, 2 stages); (2) larger glaucothoe adaptation (*C. cavipes*, *C. clypeatus*, *C. compressus* and *C. purpureus*, 4–6); (3) smaller glaucothoe adaptation (*C. rugosus* and *B. latro*, 3–5); and (4) hypersaline adaptation (*C. scaevola*, 7). However, they categorised the

species mainly based on the megalopal body length and/or adult habitats, and did not analyse the relationship between larval body length and number of zoeal stages. Our analyses implied that the number of zoeal stages was not determined by megalopal body length, but was influenced by the body length at hatching, indicating that larvae did not have longer developmental pathways to achieve the larger body length at the megalopal stage. Besides body length at hatching, growth increment at moulting was also associated with the larval developmental pathway. The relationship between parameters *a* and *b* in the linear growth equation between number of moults and body length for the species examined suggested the existence of 4 larval growth and development patterns in coenobitids: (1) species with initially smaller larvae and smaller growth increments — longer pathway (*C. cavipes* and *C. scaevola*); (2) species with initially smaller larvae and larger growth increments — shorter pathway (*C. purpureus*, *C. rugosus*, and *C. violascens*); (3) species with initially larger larvae and smaller growth increments — shorter pathway (*C. brevimanus*, *C. clypeatus*, *C. compressus*, and *B. latro*); and (4) species with initially largest larvae and smallest growth increments — shortest pathway (abbreviated development) (*C. variabilis*).

These larval growth and developmental patterns might have evolved to allow environmental adaptation by a species within phylogenetic constraints. One of the fundamental trade-offs in life-history evolution is between size and number of eggs (larvae) (Smith & Fretwell 1974). Given this, we hypothesise that coenobitid species might have evolved life-history traits with variations in the initial body length of larvae. To achieve the given size at the megalopal stage in coenobitid species, in the group with initially smaller larvae, some species with smaller growth increments had longer developmental pathways with a longer zoeal duration (Pattern 1). By contrast, some species increased growth increments, resulting in shorter developmental pathways without extending zoeal duration (Pattern 2). However, some species increased the initial body length while retaining shorter developmental pathways without extending zoeal duration, resulting in smaller growth increments (Pattern 3). In the case of the extreme phenotype in the coenobitids reported so far (Pattern 4), *C. variabilis* evolved to produce the largest larvae at hatching, resulting in abbreviated development with 2 brief, lecithotrophic zoeal stages (Harvey 1992). Although it is not known which pattern of larval growth and development is the ancestral trait, the abbreviated larval development in *C. variabilis* might be considered as a derived character, as previously suggested for some decapod crustaceans (Anger 2001, Wowor et al. 2009).

Larval duration

Total zoeal durations varied among/within coenobitid species depending on the temperatures and developmental pathways: the shortest duration was observed in *C. variabilis*, which exhibits abbreviated development (6–7 d at 30°C) (Harvey 1992), whereas the longest duration was observed in *C. scaevola*, with 7 stages (67 d at 25°C) (Al-Aidaroos & Williamson 1989). The geographical occurrence of coenobitid species can be divided into 2 patterns (Hartnoll 1988, Nakasone 1988b, Harvey 1992, Wang et al. 2007): (1) widely distributed species, *C. brevimanus*, *C. cavipes*, *C. perlatus*, *C. rugosus*, *C. violascens*, and *B. latro* in the Indo-Pacific; and (2) species with a relatively narrower distribution, *C. clypeatus* in the Western Atlantic, *C. compressus* in the west coast of America from Mexico to Chile, *C. purpureus* in the Northwestern Pacific adjacent to Japan, *C. scaevola* in the Red Sea, Gulf of Aden, Somalia, and Pakistan, and *C. variabilis* in Northern Australia. The abbreviated larval development seems to be relevant to the limited geographical distribution in *C. variabilis*. However, the narrower distribution was observed in *C. scaevola*, which has the longest developmental pathway of the studied species. Thus, larval duration was apparently unrelated to the geographical distribution of coenobitid species. Studies on the phylogeographic history and oceanographic conditions are needed for a better understanding of speciation and geographical distribution of coenobitid crabs.

Acknowledgements. We thank the Okinawa Prefectural Board of Education for permission to culture the land hermit crabs. We are grateful to the editors, Sven Thatje, and 2 anonymous reviewers for their constructive comments and suggestions, which have improved the manuscript. This study was supported by Grants-in-Aid for Scientific Research C20580198 and B24310171 from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

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Editorial responsibility: Klaus Anger, Malente, Germany

Submitted: June 19, 2014; Accepted: November 27, 2014
Proofs received from author(s): February 13, 2015