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Larval Performance of Amphidromous and Landlocked Atyid Shrimp Species in the Genus *Paratya* Under Different Temperature and Salinity Conditions

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Freshwater shrimps in the family Atyidae exhibit one of two life history traits: amphidromy, in which planktonic larvae develop in the sea; and landlocked, in which lecithotrophic larvae develop in freshwater. Temperature and salinity are the most important environmental factors that affect the survival, duration, and growth of decapod crustacean larvae. Larvae of landlocked shrimps are known to retain the ancestral habit of amphidromy, *i.e.*, the ability to develop to the juvenile stage in saline water. Faster development exhibited by large larvae of landlocked shrimps is considered an adaptation that allows the larvae to stay in or near parental habitats. Therefore, information on larval performance under different temperature and salinity conditions is essential to obtain a better understanding of population connectivity through marine larval dispersal in amphidromous shrimps as well as larval adaptation to freshwater environments in landlocked shrimps. We examined the effects of temperature and salinity on the larval performance of two closely related atyid shrimps in the genus *Paratya*: the amphidromous *P. compressa* and the landlocked *P. improvisa*. Larvae were reared under the 25 combinations of five different temperatures (20, 23, 26, 29, and 32°C) and salinity levels (4.25, 8.5, 17, 25.5, and 34 ppt). In *P. compressa*, the rate of larvae that survived into the juvenile stage decreased linearly with increasing temperature and the larvae adapted to a wider range of salinity (8.5–34 ppt), though larval mortality increased at the high salinity (34 ppt) under the higher temperature conditions. In *P. improvisa*, larval survival rates were higher under a wider range of temperatures (20–29°C) in brackish water (4.25–17 ppt). Thus, *P. compressa* larvae may disperse broadly under the high salinity conditions of the open sea, but oceanic currents with high temperature and high salinity conditions may act as a barrier to restrict larval dispersion northwards from the southern islands. *Paratya improvisa* larvae adapted to a wider range of temperatures in natural freshwater environments and larval duration was shorter in *P. improvisa* than in *P. compressa* under the wide range of temperature and salinity conditions. Our results also highlight the retention strategy by which landlocked *P. improvisa* larvae stay in or near parental habitats.

Key words: Larval survival, Larval growth, Larval dispersal strategy, Larval retention strategy, Freshwater adaptation.

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BACKGROUND

Freshwater shrimps in the family Atyidae are a highly species-rich group of decapod crustaceans (Decapoda: Caridea) that inhabit various freshwater bodies from torrential mountain streams down to sluggish, oligohaline waters and rivers or streams inside karst caves (De Grave et al. 2008; De Grave and Fransen 2011; Cai and Ng 2018). Atyid shrimps exhibit one of two life history traits: amphidromous or landlocked (Shokita 1979; Hayashi and Hamano 1984; Bauer 2013).

Amphidromous shrimps spawn many relatively small eggs (Shokita 1979; Hayashi and Hamano 1984; Bauer 2013). Their larvae require saline water for successful development (Shokita 1979; Hayashi and Hamano 1984; Nakahara et al. 2005; Kondo et al. 2021) and spend their pelagic life through longer periods of planktotrophic zoeae in the sea before migrating up into the adult freshwater habitat as juveniles (Hamano and Hayashi 1992; Hamano et al. 2005; Ideguchi et al. 2000 2007; Bauer 2013; Yatsuya et al. 2013). Accordingly, amphidromous shrimp populations are connected through marine larval dispersal (Shokita 1979; Bauer 2013; Fujita et al. 2016).

On the contrary, landlocked shrimps complete their entire life cycle within freshwater habitats. They generally spawn a relatively small number of large eggs with considerable amounts of yolk (Shokita 1979; Hayashi and Hamano 1984; Bauer 2013). These produce morphologically advanced non-feeding or facultatively lecithotrophic larvae, resulting in a shortened larval developmental period before moulting into the juvenile stage (*sensu* Møller et al. 2020), or directly producing juveniles (Shokita 1979; Hayashi and Hamano 1984; Anger 2001; Bauer 2013).

Amphidromy is considered a plesiomorphic (ancestral) life history trait in freshwater shrimps (Shokita 1979), and current evidence from physiological, developmental, and phylogenetic considerations supports the hypothesis of an evolutionary process from ancestral marine species through freshwater amphidromous to landlocked species (Bauer 2013). It has been argued that, in landlocked shrimps, non-feeding or facultative lecithotrophy of larvae are adaptations to limited food conditions in freshwater environments (Shokita 1979; Anger 2001 2006; Bauer 2013; Hamasaki et al. 2020a), and faster development and settlement behaviours that large larvae exhibit are adaptations that allow the larvae to stay in or near parental habitats in flowing waters (Shokita 1979; Mashiko 1982 1990a; Dudgeon 1985; Wong 1989; Hancock 1998; Hancock et al. 1998; Hamasaki et al. 2020a).

Temperature and salinity are the most important environmental factors known to affect the larval survival, duration, and growth of decapod crustaceans (Anger 2001 2003). There are spatial and temporal fluctuations in the water temperatures of sea- and freshwater bodies and in the salinity of seawater. Larvae of landlocked shrimps are known to be able to develop to the juvenile stage in brackish water under laboratory conditions (Ogasawara et al. 1979; Mashiko 1990b; Fidhiany et al. 1991; Imai et al. 2001; Anger and Hayd 2010; Kawamura and Akiyama 2010; Charmantier and Anger 2011). Therefore, information on larval performance under different temperature and salinity conditions is essential for a better understanding of population connectivity through marine larval dispersal in amphidromous shrimp species. Moreover, interspecific comparison of larval temperature and salinity adaptations between amphidromous and landlocked shrimps is useful to attain a better understanding of larval adaptation to freshwater environments in landlocked shrimp species. However, to the best of our knowledge, no studies have compared the temperature and salinity adaptations of larvae between closely related amphidromous and landlocked shrimp species. In the present study, we conducted larval culture experiments using two atyid shrimps in the genus *Paratya* Miers 1882: the amphidromous *P. compressa* (De Haan 1844) and the landlocked *P. improvisa* Kemp 1917.

Freshwater shrimps in the genus *Paratya* consists of 13 species (De Grave and Fransen 2011; Marin 2018). They are distributed in the North and South Pacific (Page et al. 2005), and only two closely related species, *P. compressa* and *P. improvisa*, occur in the North Pacific (Ikeda 1999; Page et al. 2005; Cai and Shokita 2006; Marin 2018). *Paratya compressa* is amphidromous with many small eggs (Ikeda 1999; Kawamura and Akiyama 2010), inhabiting the lower and middle reaches of rivers (Shokita 1979; Hamano and Hayashi 1992; Suzuki et al. 1993; Ikeda 1999; Usami et al. 2008; Saito et al. 2012). It is distributed from the southern islands in the Ryukyu Archipelago, Japan, and the southwestern region of mainland Japan through the Korean Peninsula to the Russian mainland coast of the Sea of Japan (Shokita 1979; Ikeda 1999; Marin 2018). *Paratya improvisa* is a landlocked species that produces few, relatively large eggs (Ikeda 1999; Kawamura and Akiyama 2010; Imai 2006 2014) and inhabits rivers, ponds, and lakes (Ikeda 1999; Imai 2006 2014; Usami et al. 2008; Yatsuya et al. 2012). It is distributed only in the northeastern region of mainland Japan (Ikeda 1999).

Larvae of both *Paratya* species have eight zoeal stages before moulting into the juvenile stage (Kawamura and Akiyama 2010); however, larval developmental traits differ between the amphidromous *P. compressa* and the landlocked *P. improvisa*. Newly hatched larvae are larger and the larval duration is shorter in *P. improvisa* than in *P. compressa*, and *P. improvisa* larvae exhibit settlement behaviour beginning with the early zoeal stage (Hamasaki et al. 2020a). *Paratya compressa* larvae are planktotrophic, whereas *P. improvisa* larvae are facultatively lecithotrophic, resulting in moulting to stage 3 zoeae without food (Kawamura and Akiyama 2010). *Paratya improvisa* larvae survive and develop into the juvenile stage under poor feeding conditions that are not suitable for the survival and development of *P. compressa* larvae (Hamasaki et al. 2020a). Thus, landlocked *P. improvisa* larvae adapt to limited food conditions in freshwater environments while exhibiting rapid development and behavioural characteristics to stay in or near parental habitats. However, few studies have investigated larval survival, duration of the larval stage, and growth of these species under limited temperature and salinity conditions (26°C and 17 ppt) (Hamasaki et al. 2020a).

The present study aimed to evaluate the effects of temperature and salinity on the survival, duration of the larval stage, and growth of *P. compressa* and *P. improvisa* larvae. Our results highlight the variability in temperature and salinity adaptations of the larvae of these two species, and we discuss the ecological implications in terms of the larval dispersal strategy in the amphidromous *P. compressa* and larval adaptation to freshwater habitats in the landlocked *P. improvisa*.

MATERIALS AND METHODS

Shrimp collection and culturing

Culture experiments were conducted in a laboratory at the Tokyo University of Marine Science and Technology, Tokyo, Japan, in 2018 and 2019. Wild mature female and male shrimps were captured using scoop nets at the following locations in Chiba Prefecture, Japan: *P. compressa*, Banda River (34°58'N, 139°46'E) in April 2018; and *P. improvisa*, Yoro River (35°21'N, 140°08'E) in July 2019.

Shrimps were transported to the laboratory and acclimatised overnight; then, they were cultured in aerated aquaria (23 litres) under natural photoperiod conditions (20–30 individuals per tank, unknown sex ratio). Aquarium temperature was maintained at approximately 23°C, according to the method detailed in our previous study (Hamasaki et al. 2020a). This falls within the range of summer temperatures during the reproductive season of *Paratya* species in their natural habitat (Imai 2006 2014; Saito et al. 2012; Yatsuya et al. 2012; K. Hamasaki, unpublished data).

Experimental temperature and salinity conditions

We previously conducted laboratory experiments to evaluate the larval performance of three amphidromous atyid shrimp species in the genus *Caridina* H. Milne-Edwards, 1837 (Kondo et al. 2021). In these experiments, larvae were cultured under 25 combinations of five different temperatures (20, 23, 26, 29, and 32°C) and salinity levels (4.25, 8.5, 17, 25.5, and 34 ppt). The present study was carried out in conjunction with our previous study (Kondo et al. 2021) using a limited number of temperature-controlled incubation chambers. Therefore, we adopted the same temperature and salinity levels in the present study. These temperature levels were selected according to the seawater temperature profiles (~20–31°C) around the Japanese coastal areas (Japan Meteorological Agency 2021) during the reproductive season of the *Caridina* shrimps (Shokita 1979; Hamano and Hayashi 1992; Ideguchi et al. 2000; Hamano et al. 2005; Yamahira et al. 2007; Yatsuya et al. 2013). Salinity levels were also set assuming the salinity profiles from the river mouth to the open sea, where *Caridina* larvae may develop (Ideguchi et al. 2000; Yatsuya et al. 2013; Urakawa et al. 2015). Pure freshwater treatment was not employed because the saline water used for culturing live foods could not be removed when the live foods were added to the larval culture medium. The reproductive season of *P. compressa* begins and terminates earlier than that of *Caridina* shrimps (Shokita 1979; K. Hamasaki, unpublished data), and wide temperature measurements ranging from 15 to 31°C were recorded during spring and summer in natural habitats where *P. improvisa* larvae were collected (Imai 2006 2014). Therefore, the lower temperature to which larvae of the two *Paratya* species were adapted could not be evaluated under the minimum temperature setting (20°C) in our experiments. Nevertheless, our experiments detected interspecific and intergeneric variabilities in the larval thermal adaptation of atyid shrimps (see the RESULTS and DISCUSSION sections).

Larvae were cultured in temperature-controlled incubation chambers with a 14:10-h light:dark photoperiod (MT1-201, Tokyo Rikakikai Co. Ltd., Tokyo, Japan). Larval rearing water with different salinities was prepared using dechlorinated tap water and artificial sea salts (Sealife, Marinetech Co. Ltd., Tokyo, Japan). Rearing temperatures were recorded every 30 min during the larval culture period of each species using data loggers (Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan) placed in the larval culture containers. The mean ± standard deviation values of actual larval rearing temperatures were as follows: *P. compressa*, 19.9 ± 0.4°C, 23.0 ± 0.4°C, 26.0 ± 0.3°C, 26.5 ± 0.4°C, and 33.3 ± 0.4°C; *P. improvisa*, 20.5 ± 0.3°C, 23.5 ± 0.6°C, 26.9 ± 0.3°C, 29.8 ± 0.2°C, and 32.9 ± 0.3°C.

Larval culture

Twelve stage 1 zoeae from a single *P. compressa* female and twelve stage I zoeae (six each) from two brooding females of *P. improvisa* were used for each temperature and salinity combination because the fecundity is high in *P. compressa* but relatively low in *P. improvisa*. The larval hatching date of each species-brood was as follows: *P. compressa*, May 17, 2018; *P. improvisa* brood 1, July 27, 2019; and *P. improvisa* brood 2, August 4, 2019.

Stage 1 zoeae from each brood were sampled, fixed with 5% neutral formalin for one day, and then preserved in 70% ethanol. The carapace length of ten specimens of each species-brood was measured from the posterior margin of sessile eyes to the posterior end of the carapace (Nakahara et al. 2007) using a microscope equipped with a digital camera and an image analysing system (Nikon Digital Sight and NIS-Elements software, Nikon Corp., Tokyo, Japan). The carapace length of stage 1 zoeae (mean ± standard deviation) of *P. compressa* was 0.313 ± 0.012 mm, and that of the *P. improvisa* broods 1 and 2 was 0.698 ± 0.036 mm and 0.679 ± 0.041 mm, respectively.

Larvae were housed individually in the wells of six-well cell culture plates, which contained 8 ml artificial saline water per well. Larvae were fed euryhaline phytoplankton *Tetraselmis* sp. at 1×10^5 cells ml^{-1} and euryhaline zooplankton, the rotifer *Brachionus plicatilis* species complex (small-morphotype), at 20 $individuals \cdot ml^{-1}$. Both of these are effective foods for the culture of atyid shrimp larvae (Hamasaki et al. 2020a b). *Tetraselmis* sp. and rotifers were cultured at 34 ppt and 24 ppt, respectively, according to the methods detailed in our previous studies (Hamasaki et al. 2020a b).

Every morning, larvae were transferred to clean culture wells with fresh saline water and food using a glass pipette, and the numbers of living and dead larvae were recorded under a stereomicroscope. The moulting events were not considered as larval performance in the present study because the fragile exuviae of small larvae were easily lost or overlooked during the culture operations in our previous culture experiments using atyid shrimp larvae (Hamasaki et al. 2020a b). In *P. compressa*, each zoeal larva each cultured at temperature/salinity conditions of 19.9°C/17 ppt, 19.9°C/34 ppt, 23.0°C/34 ppt, 26.0°C/4.25 ppt, and 33.3°C/34 ppt and three zoeal larvae cultured at 26.0°C/8.5 ppt were accidentally lost during the culture operations These larvae were excluded from subsequent analysis.

Larval rearing was terminated when all surviving larvae had moulted to the juvenile stage. We observed later-stage larvae under the stereomicroscope and determined whether they moulted to the juvenile stage based on their behaviour as well as the external morphology. Larvae were considered to reach the juvenile stage when they were able to steadily settle on the bottom of a rearing container using the endopods of the pereiopods and swim in the normal manner using pleopods for propulsion, while showing the morphological characteristics of the first and second antennae of the first juvenile stage, as described by Kawamura and Akiyama (2010). The final survival rate of larvae was defined for each temperature-salinity combination in each species as: (number of larvae that moulted into the juvenile stage)/(number of initial larvae) × 100.

Surviving juveniles of each species were fixed and preserved similar to the stage 1 zoea specimens, and the carapace length was measured from the posterior margin of the orbit to the posterior end of the carapace (Nakahara et al. 2007). One *P. improvisa* specimen reared at 29.8°C/4.25 ppt was not measured because of damage to its carapace.

Statistical analysis

Statistical analyses were performed using R statistical software (R4.0.2; R Core Team 2020) at a 5% significance level. Data for *P. improvisa* larvae hatched from two broods were combined for subsequent analysis. A generalised linear model (GLM) with a binomial distribution was employed to evaluate the influences of temperature and salinity on larval survival to moult into the juvenile stage [*i.e.*, the binary survival (1) or death (0)] (response variable). We also used the Poisson-GLM and a general linear model (LM) to evaluate the effects of temperature and salinity on larval duration (*i.e.*, the number of days required to moult into the juvenile stage) and larval growth (*i.e.*, the carapace length of juveniles) (response variables), respectively.

In the GLM and LM analyses, we applied four models for which the continuous explanatory variables included mean temperature (T) and salinity (S) for culturing larvae, or their interaction term ($T \times S$) and/or quadratic terms (T^2 and S^2), considering their interactions and nonlinear effects: model 1, $y \sim T + S + T^2 + S^2 + T \times S$; model 2, $y \sim T + S + T^2 + S^2$; model 3, $y \sim T + S + T \times S$; and model 4, $y \sim T + S$. The model with the lowest Bayesian information criterion (BIC) value (Schwarz 1978) was then selected as the best to describe the effects of temperature and salinity on larval performance in each species. The coefficients of the models were estimated, and their statistical significance was evaluated using the *glm* function for binomial (logit link) and Poisson (log link) GLM analyses and the *lm* function for LM analyses.

For interspecific comparison of survival response to different temperatures and salinities, the response-surface contour plots of final survival rate were generated using the *contour* function based on the calculations derived by substituting the designated temperature (18–35°C, 0.5°C interval) and salinity (4–36 ppt, 1 ppt interval) combinations into the selected model equation for each species.

RESULTS

Larval survival

In *P. compressa*, larvae could survive to moult to the juvenile stage at 19.9–29.5°C and 8.5–34 ppt (Fig. 1A), but all the larvae died 6–20 days after hatching at 33.3°C and 4.25 ppt (see supplementary figure S1 for survival rate and moulting rate of larvae in relation to days after hatching of the larvae of *P. compressa*). Among the four models that were applied to evaluate the effects of temperature and salinity on larval survival, model 1 ($y \sim T + S + T^2 + S^2 + T \times S$) was selected as the best (Table 1), and the coefficient estimates of explanatory variables were statistically significant except for the linear and quadratic terms of temperature. The final survival rate of larvae was the highest at 19.9°C, showing a linear decrease with increasing temperature at all salinity levels (Fig. 1A). The relationship between salinity and final survival rate tended to be represented by a convex curve at all temperature levels, while the salinity range associated with the highest survival rate tended to decrease with increasing temperature, as exemplified by the statistically significant coefficient estimate of the interaction term ($T \times S$) (Table 1).

Paratya improvisa larvae tended to stay on the bottom of the rearing container from the early zoeal stage. Larvae exhibited higher final survival rates under temperature-salinity combinations within 20.5–29.8°C and 4.25–17 ppt (Fig. 1B). At 32.9°C, they could reach the juvenile stage only at 8.5 ppt, showing a high survival rate. All larvae died within 2 days of hatching at 34 ppt (see supplementary figure S2 for survival rate and moulting rate of larvae in relation to days after hatching of the larvae of *P. improvisa*). Also, nearly all larvae died between 1 and 18 days after hatching at 25.5 ppt, except for a few that survived to the juvenile stage at 26.9°C–25.5 ppt (Fig. 1B). Model 2 ($y \sim T + S + T^2 + S^2$) was selected as the best to describe the effects of temperature and salinity on larval survival of *P. improvisa*, and all the coefficients of linear and quadratic terms were statistically significant (Table 1).

The larval survival response to temperature and salinity conditions thus varied between the two *Paratya* species, and the response-surface contour plots of final survival rates well illustrated the interspecific variability (Fig. 2). *Paratya compressa* larvae adapted to lower temperatures and a wider range of salinity, whereas *P. improvisa* larvae adapted to a wider range of temperatures and lower salinity conditions.

Larval duration

Larval duration tended to decrease with increasing temperature in both species (Fig. 3). Models 4 ($y \sim T + S$) and 2 ($y \sim T + S + T^2 + S^2$) were selected as the best models to describe the effects of temperature and salinity on larval duration for *P. compressa* and *P. improvisa*, respectively (Table 1), and the coefficient estimates of the linear and quadratic terms were statistically significant for temperature but not for salinity. Larval duration was shorter in *P. improvisa* than in *P. compressa* at all temperature and salinity combinations.

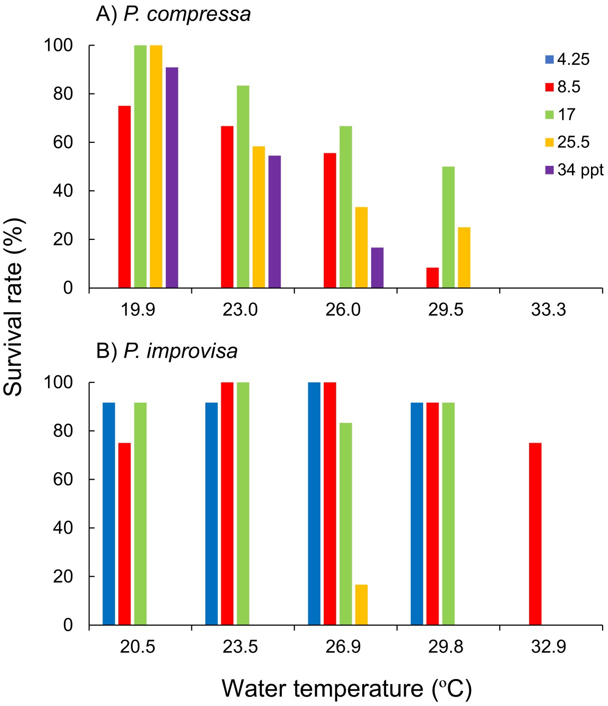

Fig. 1. Final larval survival rates to moult into the juvenile stage of *Paratya compressa* (A) and *Paratya improvisa* (B). Larvae were reared under the 25 combinations of five different temperatures (*x* axis) and salinities (different coloured bars).

Larval growth

Model 4 ($y \sim T + S$) was selected as the best to describe the effects of temperature and salinity on larval growth in both species (Table 1), but the salinity level did not significantly affect larval growth. Temperature exhibited a significant negative effect on larval growth (Table 1), but the carapace length of juveniles varied less between different temperature levels (Fig. 4).

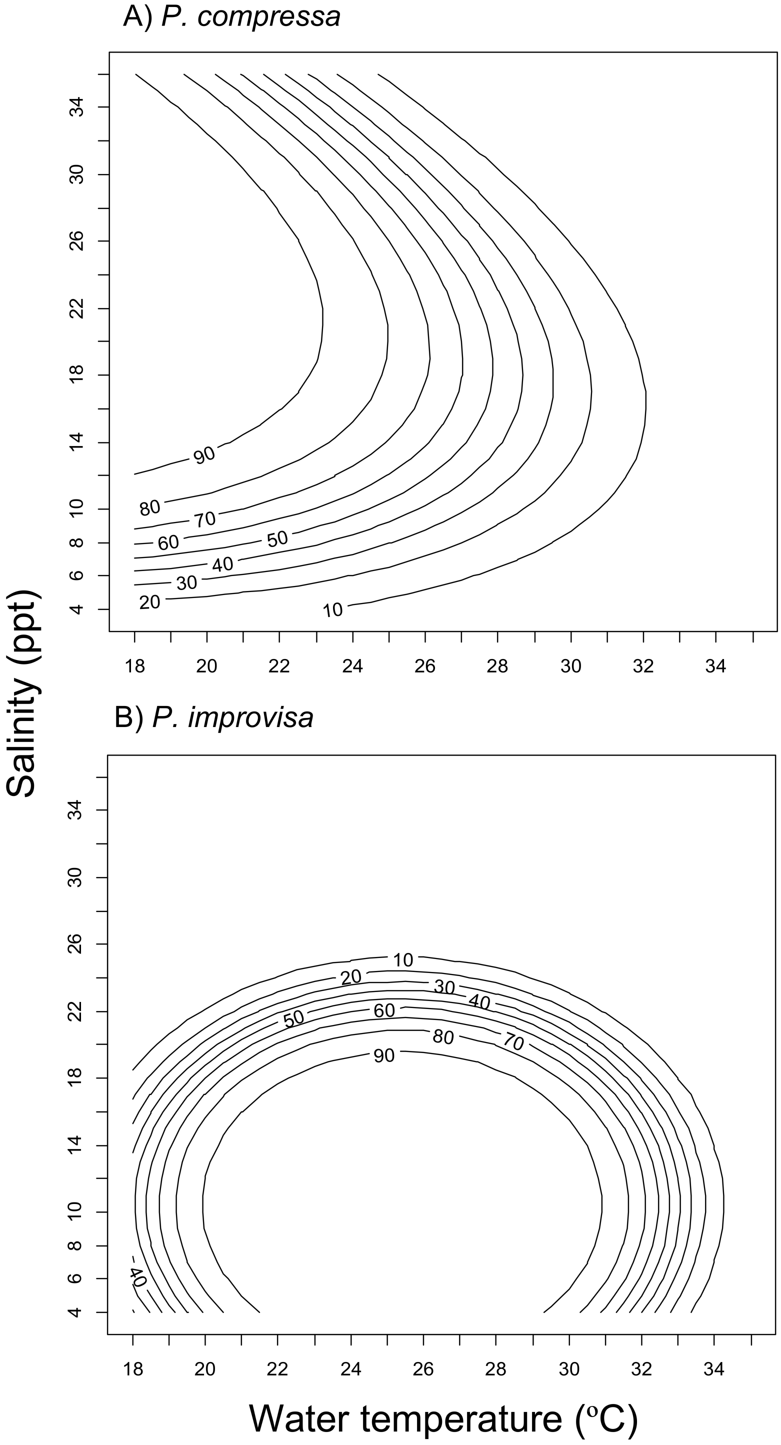

Fig. 2. Response-surface contour plots of larval survival rates at different combinations of temperature and salinity conditions in *Paratya compressa* (A) and *Paratya improvisa* (B).

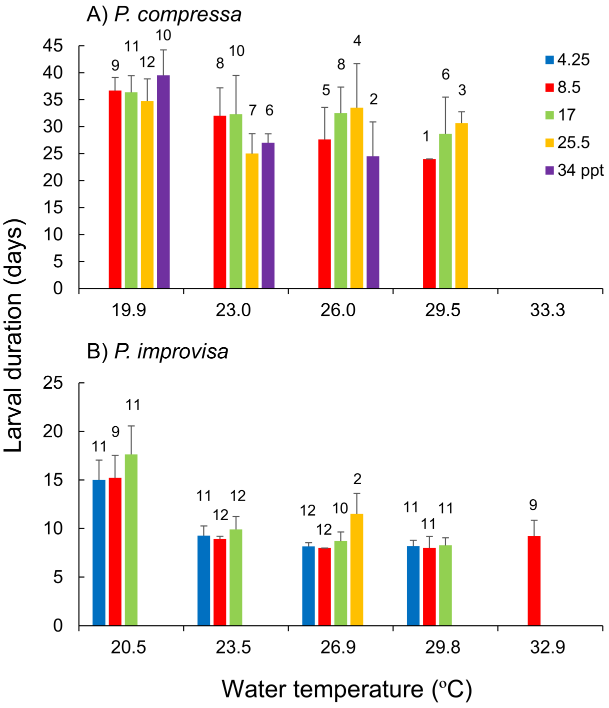

Fig. 3. Number of days required to moult into the juvenile stages (larval duration) of *Paratya compressa* (A) and *Paratya improvisa* (B). Larvae were reared under 25 combinations of five different temperatures (x axis) and salinities (different coloured bars). Numbers of individuals are shown above the bars.

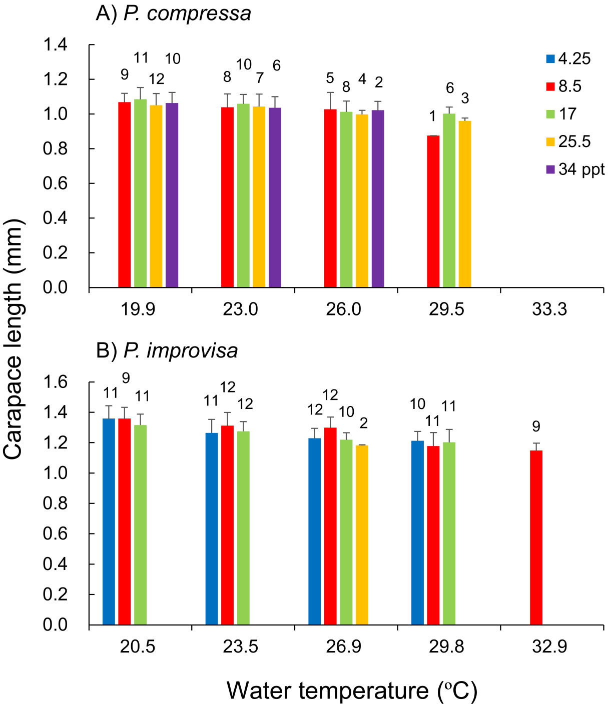

Fig. 4. Carapace length of juveniles of *Paratya compressa* (A) and *Paratya improvisa* (B). Larvae were reared under 25 combinations of five different temperatures (x axis) and salinities (different coloured bars). Numbers of individuals are shown above the bars.

Table 1. Coefficient estimates with standard errors (SE) for the explanatory variables in the generalised linear model (GLM) or linear model (LM) to best describe the effects of temperature (T) and salinity (S) on larval survival (alive or not) and duration to reach the juvenile stage (days), and carapace length (mm) of juveniles of two atyid shrimp species in the genus *Paratya*. Four models were applied in the binomial- and Poisson-GLM analyses for larval survival and larval duration, respectively, and those in the LM analysis for the carapace length: model 1, $y \sim T + S + T^2 + S^2 + T \times S$; model 2, $y \sim T + S + T^2 + S^2$; model 3, $y \sim T + S + T \times S$; and model 4, $y \sim T + S$. The model with the minimum Bayesian information criterion (BIC) value was selected as the best model for each larval performance in each species. See supplementary tables S1 and S2 for the coefficient estimates and BIC values of all models for *P. compressa* and *P. improvisa*, respectively

		Larval survival				Larval duration				Carapace length			
Species	Coefficient	Estimate	SE	z value	P	Estimate	SE	z value	P	Estimate	SE	t value	P
P. compressa	Intercept	-8.2399	8.2438	-1.000	0.3175	4.1679	0.1438	28.992	< 0.0001	1.2629	0.0497	25.411	< 0.0001
	T	0.4032	0.6425	0.628	0.5303	-0.0290	0.0058	-5.003	< 0.0001	-0.0093	0.0020	-4.698	< 0.0001
	S	1.0352	0.1857	5.575	< 0.0001	-0.0011	0.0020	-0.550	0.5830	-0.0004	0.0007	-0.618	0.5380
	T^2	-0.0105	0.0124	-0.847	0.3968								
	S^2	-0.0151	0.0024	-6.266	< 0.0001								
	$T \times S$	-0.0171	0.0059	-2.898	0.0038								
P. improvisa	Intercept	-58.4198	12.1570	-4.805	< 0.0001	11.6631	1.2831	9.090	< 0.0001	1.6708	0.0444	37.616	< 0.0001
	T	4.7067	0.9352	5.033	< 0.0001	-0.6802	0.1002	-6.791	< 0.0001	-0.0153	0.0016	-9.354	< 0.0001
	S	0.6937	0.1589	4.365	< 0.0001	-0.0237	0.0234	-1.013	0.3110	-0.0017	0.0011	-1.452	0.1490
	T^2	-0.0926	0.0176	-5.273	< 0.0001	0.0121	0.0019	6.212	< 0.0001				
	S^2	-0.0332	0.0060	-5.559	< 0.0001	0.0014	0.0010	1.464	0.1430				

DISCUSSION

Interspecific variability in the larval survival response

Our larval culture experiments demonstrated that temperature and salinity significantly affected larval survival for the two *Paratya* species with different life history traits: the amphidromous *P. compressa* and the landlocked *P. improvisa* (Fig. 1). In *P. compressa* larvae, the highest final survival rate to the juvenile stage was found at the lowest temperature of 19.9°C, and the final survival rate decreased with increasing temperature, until no larvae survived to the juvenile stage at the highest temperature of 33.3°C. *Paratya compressa* larvae could survive to the juvenile stage at ≥ 8.5 ppt salinities, but the larval survival response to salinity changed with temperature. There was a large decreasing trend in final survival rates with increasing temperature at salinities of 25.5 and 34 ppt. On the contrary, *P. improvisa* larvae exhibited higher final survival rates at salinities of 4.25–17 ppt at a wider temperature range (20.5–29.8°C), and almost all died at salinities of 25.5 and 34 ppt. Interspecific variability in the larval survival response to temperature and salinity is thus evident between the amphidromous *P. compressa* and the landlocked *P. improvisa*.

Larval dispersal strategy in *P. compressa*

Kondo et al. (2021) cultured three species of amphidromous atyid shrimp larvae from the genus *Caridina*, namely, *C. leucosticta* Stimpson 1860, *C. multidentata* Stimpson 1860, and *C. typus* H. Milne-Edwards 1837, at different temperature and salinity combinations similar to those used in the present study to evaluate their temperature and salinity adaptations. They demonstrated that higher larval survival was achieved at around 26°C in all species, and only *C. leucosticta* larvae were able to survive to the juvenile stage at the lower salinity condition of 8.5 ppt. They also found that *C. multidentata* larvae exhibited an ability to adapt to a wide range of salinity conditions (17–34 ppt), and *C. typus* larvae adapted to the higher salinity condition of 34 ppt better than *C. leucosticta* larvae. In the present study, the optimum temperature for larval survival could not be determined for the amphidromous *P. compressa* because they achieved the highest survival rates at the lowest temperature level (approximately 20°C) while showing higher survival rates at 8.5–34 ppt salinity (Figs. 1 and 2). Thus, *P. compressa* larvae adapted to the lower temperature and wider range of salinity compared with the amphidromous *Caridina* species.

Paratya compressa and the three *Caridina* species commonly occur in southwestern Japan (Shokita 1979; Hamano and Hayashi 1992; Suzuki et al. 1993; Ikeda 1999; Usami et al. 2008; Saito et al. 2012), and the occurrence of ovigerous *P. compressa* females begins and terminates earlier in the annual reproductive season of the atyid shrimps extending from spring to summer or early autumn (Shokita 1979; K. Hamasaki, unpublished data). Therefore, *P. compressa* larvae may adapt to the lower temperature conditions at around 15°C in the sea (Japan Meteorological Agency 2021) during the early hatching season among the atyid shrimp species.

Larvae of amphidromous shrimps develop in the brackish waters of estuaries and coastal bays or in the open sea (Shokita 1979; Hayashi and Hamamo 1984; Ideguchi et al. 2000 2007; Hamano et al. 2005; Bauer 2013; Yatsuya et al. 2013). It has been suggested that amphidromous *Caridina* species requiring lower salinities for larval development exhibit restricted larval dispersal, resulting in a genetically heterogenous population structure, and *vice versa* (Fujita et al. 2016; Kondo et al. 2021). *Paratya compressa* larvae are expected to have wide sea dispersion because of their adaptations to a wide range of salinity conditions. This is also inferred from the larval feeding habit (Hamasaki et al. 2020a). *Paratya compressa* larvae could survive and develop into the juvenile stage under poor feeding conditions compared with those of the *Caridina* species (Hamasaki et al. 2020a b), thus enabling wide larval dispersion in oligotrophic environments in coastal and offshore sea (Hamasaki et al. 2020a). *Paratya compressa* is distributed in the North Pacific from southern islands in the Ryukyu Archipelago, Japan (24°N, 123°E), in the southwestern region of mainland Japan throughout the Korean Peninsula, to the Russian mainland coast in the Sea of Japan (43°N, 133°E) (Shokita 1979; Ikeda 1999; Marin 2018). Allozyme studies demonstrate a genetically homogenous population structure of *P. compressa* throughout western Japan (Ikeda 1999) and Russian and Japanese samples of *P. compressa* have been found to have a very small pairwise genetic distance in the mitochondrial DNA cytochrome *c* oxidase subunit I (mtDNA *COI*) gene (Marin 2018), suggesting a wide larval dispersion in the sea connecting the populations. On the one hand, analyses of both the allozyme and mtDNA *COI* gene suggest the existence of a genetically distinct *P. compressa* population in the Ryukyu Archipelago (Ikeda 1999; Marin 2018). The Kuroshio Current plays an important role in transferring larvae of southern marine organisms from warmer to cooler latitudes through the Ryukyu Archipelago (24–30°N, 123–131°E) in the northwestern Pacific region (Veron and Minchin 1992; Iida et al. 2010; Soeparno et al. 2012; He et al.

2015; Chang et al. 2018; Sanda et al. 2019). *Paratya compressa* larvae adapt to lower temperature conditions, and their survival rates may decrease greatly at offshore salinity (34 ppt) when the temperature conditions are higher (Fig. 1A). Therefore, subtropical/tropical ocean climate in the Ryukyu Archipelago (Nishimura 1992) may restrict the northward ocean dispersal of *P. compressa* larvae.

Larval adaptations to freshwater habitats in *P. improvisa*

Paratya improvisa larvae exhibited higher survival rates at a wider range of temperature conditions compared with *P. compressa* larvae (Fig. 1). Temperature may fluctuate greatly in various freshwater systems where *P. improvisa* larvae may develop, and a wide range of temperature measurements (15–31°C) was recorded during spring and summer in natural habitats where *P. improvisa* larvae were collected (Imai 2006 2014). Thus, *P. improvisa* larvae adapt to a wider range of temperatures in natural freshwater environments.

The faster development and settlement behaviours exhibited by morphologically advanced non-feeding or facultatively lecithotrophic larvae of landlocked shrimps are considered adaptations that allow them to stay in or near parental habitats in flowing waters (Shokita 1979; Mashiko 1982 1990a; Dudgeon 1985; Wong 1989; Hancock 1998; Hancock et al. 1998). We previously reported that *P. improvisa* larvae have a larger hatching size and shorter developmental duration than *P. compressa* larvae, and we also noted the larval settlement behaviour beginning with the early zoeal stage in *P. improvisa* under limited conditions of temperature and salinity (26°C and 17 ppt) (Hamasaki et al. 2020a). The present study demonstrated that larval duration was shorter in *P. improvisa* than in *P. compressa* under a wide range of temperature and salinity conditions (20–29°C and 4.5–25.5 ppt) (Fig. 3). The larger body size (carapace length) of stage 1 zoeae was more evident in *P. improvisa* (0.7 mm) than in *P. compressa* (0.3 mm), and the larval settlement behaviour was observed from the early zoeal stage. The present study thus further highlight strategies that landlocked *P. improvisa* larvae use to stay in or near parental habitats. Larval growth was negatively influenced from temperature in both *Paratya* species (Table 1), but intra- and interspecific variations in the carapace length of juveniles were small (Fig. 4), suggesting the existence of a threshold size in *Paratya* species juveniles.

Larvae, which include all the zoeal stages and juveniles of *P. improvisa*, are found in freshwater environments (Yokoya 1931; Imai 2006 2014). Nevertheless, *P. improvisa* larvae have the ability to survive and develop into the juvenile stage in saline waters, excluding the higher salinity conditions (Fig. 1). A similar phenomenon has been observed among landlocked shrimps belonging to the family Palaemonidae Rafinesque 1815, such as *Macrobrachium nipponense* (De Haan 1849) (Ogasawara et al. 1979; Imai et al. 2001), *Macrobrachium pantanalense* Dos Santos, Hayd & Anger 2013 (Anger and Hayd 2010; Charmantier and Anger 2011), and *Palaemon paucidens* De Haan, 1844 (Mashiko 1990b; Fidhiany et al. 1991). In these landlocked shrimps, larvae show higher survival rates when reared in brackish waters compared to pure freshwater. This may be also the case for *P. improvisa*, since the larvae could survive to the juvenile stage only at 8.5 ppt salinity under high temperature conditions of 32.9°C (Fig. 1). The energetic cost for hyper-osmoregulation might be related to the lower survival rate of landlocked shrimp larvae in freshwater than in brackish water (Mashiko 1990b; Anger 2001 2003).

In *P. improvisa* populations inhabiting the lower reaches of rivers, larvae may be accidentally swept away with floodwaters into the sea. They would be able to survive and develop into the juvenile stage in brackish water and may recruit to populations in different freshwater bodies. Ikeda (1999) suggests that *P. improvisa* consists of many local populations showing highly genetic differentiation. Consequently, larval retention strategies of *P. improvisa* may perform well to complete an entire freshwater life cycle within the local population.

CONCLUSIONS

Our larval culture experiments highlight that temperature and salinity differentially affect the larval performance of amphidromous and landlocked atyid shrimp species. Larvae of amphidromous *P. compressa* adapt to conditions with lower temperatures and wider ranges of salinity. Larvae of landlocked *P. improvisa* adapt to a wider temperature range and lose the ability to survive to the juvenile stage at higher salinity conditions. These larval traits are considered to affect population connectivity via larval dispersal in the sea in *P. compressa*, and they are adaptations to freshwater environments in *P. improvisa*. Larval temperature and salinity adaptations are thus important ecological keys to understand life history traits in atyid shrimp species.

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Authors' contributions: KH designed the study. SK performed the laboratory experiments. KH and SD analysed the data and prepared the manuscript. All authors approved the final manuscript.

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REFERENCES

Anger K. 2001. The biology of decapod crustacean larvae. Crustacean Issues 14. A.A. Balkema, Lisse, The Netherland.

Anger K. 2003. Salinity as a key parameter in the larval biology of decapod crustaceans. Invertebr Reprod Dev **43:**29–45. doi:10.1080/07924259.2003.9652520.

Anger K. 2006. Contribution of larval biology to crustacean research: a review. Invertebr Reprod Dev **49:**175–205. doi:10.1080/07924259.2006.9652207.

Anger K, Hayd L. 2010. Feeding and growth in early larval shrimp *Macrobrachium amazonicum* from the Pantanal, southwestern Brazil. Aquat Biol **9:**251-261. doi:10.3354/ab00259.

Bauer RT. 2013. Amphidromy in shrimps: a life cycle between rivers and the sea. Lat Am J Aquat Res **41:**633−650. doi:10.3856/vol41-issue4-fulltext-2.

Cai Y, Ng PKL. 2018. Freshwater shrimps from karst caves of southern China, with descriptions of seven new species and the identity of *Typhlocaridina linyunensis* Li and Luo, 2001 (Crustacea: Decapoda: Caridea). Zool Stud **57:**27. doi:10.6620/ZS.2018.57-27.

Cai Y, Shokita S. 2006. Atyid shrimps (Crustacea: Decapoda: Caridea) of the Ryukyu Islands, southern Japan, with descriptions of two new species. J N Hist **40:**2123–2172. doi:10.1080/00222930601084049.

Chang Y-LK, Miyazaki Y, Miller MJ, Tsukamoto K. 2018. Potential impact of ocean circulation on the declining Japanese eel catches. Sci Rep **8:**5496. doi:10.1038/s41598-018-23820-6.

Charmantier G, Anger K. 2011. Ontogeny of osmoregulatory patterns in the South American shrimp *Macrobrachium amazonicum*: loss of hypo-regulation in a land-locked population indicates phylogenetic separation from estuarine ancestors. J Exp Mar Biol Ecol **396:**89–98. doi:10.1016/j.jembe.2010.10.013.

De Grave S, Cai Y, Anker A. 2008. Global diversity of shrimps (Crustacea: Decapoda: Caridea) in freshwater. Hydrobiologia **595:**287–293. doi:10.1007/s10750-007-9024-2.

De Grave S, Fransen CHJM. 2011. Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). Zool Meded **85:**195–589.

Dudgeon D. 1985. The population dynamics of some freshwater carideans (Crustacea: Decapoda) in Hong Kong, with special reference to *Neocaridina serrata* (Atyidae). Hydrobiologia **120:**141–149. doi:10.1007/BF00032135.

Fidhiany L, Kijima A, Fujino Y. 1991. Adult salinity tolerance and larval salinity requirement of the freshwater shrimp *Palaemon paucidens* in Japan. Tohoku J Agr Res **42:**17–24.

Fujita J, Zenimoto K, Iguchi A, Kai Y, Ueno M, Yamashita Y. 2016. Comparative phylogeography to test for predictions of marine larval dispersal in three amphidromous shrimps. Mar Ecol Prog Ser **560:**105–120. doi:10.3354/meps11911.

Hamano T, Hayashi K. 1992. Ecology of an atyid shrimp *Caridina japonica* (De Man, 1892) migrating to upstream habitats in the Shiwagi Rivulet, Tokushima Prefecture. Crust Res **21:**1−13. doi:10.18353/rcustacea.21.0_1. (in Japanese with English abstract)

Hamano T, Ideguchi K, Nakata K. 2005. Larval drift and juvenile recruitment of amphidromous freshwater shrimps (Decapoda: Caridea) in the Nishida River, western Japan. Aquacult Sci **53:**439–446. doi:10.11233/aquaculturesci1953.53.439. (in Japanese with English abstract)

Hamasaki K, Nishimoto S, Okada M, Kimura A, Otsubo K, Dan S. 2020b. Dietary effects of phytoplankton and zooplankton on larval survival, duration and growth of four *Caridina* species (Decapoda: Caridea: Atyidae) under laboratory conditions. Crust Res **49:**225–236. doi:10.18353/crustacea.49.0_225.

Hamasaki K, Okada M, Nishimoto S, Dan S. 2020a. Larval performance of amphidromous and landlocked atyid shrimp species in the genus *Paratya* under different feeding conditions. Zool Stud **59:**70. doi:10.6620/ZS.2020.59-70.

Hancock MA. 1998. The relationship between egg size and embryonic and larval development in the freshwater shrimp *Paratya australiensis* Kemp (Decapoda: Atyidae). Fresh Biol **39:**715–723. doi:10.1046/j.1365-2427.1998.00323.x.

Hancock MA, Hughes JM, Bunn SE. 1998. Influence of genetic and environmental factors on egg and clutch sizes among populations of *Paratya australiensis* Kemp (Decapoda: Atyidae) in upland rainforest streams, south-east Queensland. Oecologia **115:**483–491. doi:10.1007/s004420050545.

Hayashi K, Hamano T. 1984. The complete larval development of *Caridina japonica* De Man (Decapoda, Caridea, Atyidae) reared in the laboratory. Zool Sci **1:**571–589.

He L, Mukai T, Chu KH, Ma Q, Zhang J. 2015. Biogeographical role of the Kuroshio Current in the amphibious mudskipper *Periophthalmus modestus* indicated by mitochondrial DNA data. Sci Rep **5:**15645. doi:10.1038/srep15645.

Ideguchi K, Hamano T, Nakata K. 2007. Timing of egg hatch of amphidromous freshwater shrimps in a small river (the Nishida River), western Japan. Fish Sci **73:**961−963. doi:10.1111/j.1444-2906.2007.01420.x.

Ideguchi K, Shibata Y, Kikkawa T. 2000. Larval distribution of amphidromous atyid shrimps (Decapoda: Caridea: Atyidae) in the estuary of the Yukinoura River, Japan. Trans Nagasaki Biol Soc **51:**5−13.

Iida M, Zenimoto K, Watanabe S, Kimura S, Tsukamoto K. 2010. Larval transport of the amphidromous goby *Sicyopterus japonicus* by the Kuroshio Current. Coast Mar Sci **34:**42–46.

Ikeda M. 1999. Genetic analyses for the problem of species *Paratya compressa* (Decapoda: Atyidae). Aquabiology **21:**299–307. (in Japanese with English abstract)

Imai T. 2006. Reproduction and growth of the freshwater shrimp, *Paratya compressa improvisa* in the Tsurugata Marsh, Akita Prefecture. Aquacult Sic **54:**171–178. doi:10.11233/aquaculturesci1953.54.171. (in Japanese with English abstract)

Imai T. 2014. Population structure, reproduction and growth of the freshwater shrimp, *Paratya improvisa* Kemp, 1917 (Crustacea: Decapoda: Atyidae) in Tsuruga pond, Shizuoka Prefecture, Japan. Bull Biogeogr Soc Japan **69:**91–103. (in Japanese with English abstract)

Imai T, Akiyama N, Kosaka M. 2001. Allowable salinity for survival of three types of *Macrobrachium nipponense* larvae. Aquacult Sci **49:**35–40. doi:10.11233/aquaculturesci1953.49.35. (in Japanese with English abstract)

Japan Meteorological Agency. 2021. 10-day mean sea surface temperatures. https://www.data.jma.go.jp/gmd/kaiyou/data/db/kaikyo/jun/sst_HQ.html. Accessed 14 May 2021.

Kawamura T, Akiyama N. 2010. Larval development and salinity response of two species of fresh water shrimps *Paratya compressa*, *P. improvisa*, living in Shizuoka Prefecture. Aquacult Sci **58:**127–133. doi:10.11233/aquaculturesci.58.127. (in Japanese with English abstract)

Kondo S, Hamasaki K, Dan S. 2021. Larval performance of three amphidromous shrimp species in the genus *Caridina* (Decapoda: Caridea: Atyidae) under different temperature and salinity conditions. Crust Res **50:**41–54. doi:10.18353/crustacea.50.0_41.

Marin I. 2018. On the taxonomic status of amphidromous shrimp *Paratya borealis* Volk, 1938 (Crustacea: Decapoda: Atyidae) from the south of the Russian Far East. Zootaxa **4444:**154–162. doi:10.11646/zootaxa.4444.2.4.

Mashiko K. 1982. Differences in both the egg size and the clutch size of the freshwater prawn *Palaemon paucidens* De Hann in the Sagami River. Japan J Ecol **32:**445–451. doi:10.18960/seitai.32.4_445.

Mashiko K. 1990a. Diversified egg and clutch sizes among local populations of the fresh-water prawn *Macrobrachium nipponense* (De Haan). J Crust Biol **10:**306–314. doi:10.1163/193724090X00113.

Mashiko K. 1990b. A preliminary report on adaptedness to freshwater medium in the freshwater prawn *Palaemon* (*Palaemon*) *paucidens* De Haan. Benthos Res **38:**1–6. doi:10.5179/benthos1981.1990.1. (in Japanese with English abstract)

Møller OS, Anger K, Guerao G. 2020. Patterns of larval development. *In*: Anger K, Harzsch S, Thiel M (eds) Developmental biology and larval ecology, The Natural History of the Crustacea, Vol. 7. Oxford University Press, New York, NY, USA, pp. 165–194.

Nakahara Y, Hagiwara A, Miya Y, Hirayama K. 2005. Larval rearing of three amphidromous shrimp species (Atyidae) under different feeding and salinity conditions. Aquacult Sci **53:**305–310. doi:10.11233/aquaculturesci1953.53.305. (in Japanese with English abstract)

Nakahara Y, Hagiwara A, Miya Y, Hirayama K. 2007. Larval development of three amphidromous shrimp species (Atyidae). Bull Fac Fish Nagasaki Univ **88:**43−59. (in Japanese with English abstract)

Nishimura S. 1992. Guide to seashore animals of Japan with color pictures and key, Vol. I. Hoikusha, Osaka, Japan. (in Japanese)

Ogasawara Y, Koshio S, Taki Y. 1979. Responses to salinity in larvae from three local populations of the freshwater shrimp, *Macrobrachium nipponense*. Nippon Suisan Gakkaishi **45:**937−943. doi:10.2331/suisan.45.937.

Page TJ, Baker AM, Cook BD, Hughes JM. 2005. Historical transoceanic dispersal of a freshwater shrimp: the colonization of the South Pacific by the genus *Paratya* (Atyidae). J Biogeogr **32:**581–593. doi:10.1111/j.1365-2699.2004.01226.x.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at https://www.R-project.org/. Accessed 22 June 2020.

Saito M, Yamashiro T, Hamano T, Nakata K. 2012. Factors affecting distribution of freshwater shrimps and prawns in the Hiwasa River, southern central Japan. Crust Res **41:**27–46. doi:10.18353/crustacea.41.0_27.

Sanda S, Hamasaki K, Dan S, Kitada S. 2019. Expansion of the northern geographical distribution of land hermit crab populations: colonization and overwintering success of *Coenobita purpureus* on the coast of the Boso Peninsula, Japan. Zool Stud **58:**25. doi:10.6620/ZS.2019.58-25.

Soeparno, Nakamura Y, Shibuno T, Yamaoka K. 2012. Relationship between pelagic larval duration and abundance of tropical fishes on temperate coasts of Japan. J Fish Biol **80:**346–357. doi:10.1111/j.1095-8649.2011.03175.x.

Schwarz G. 1978. Estimating the dimension of a model. Ann Stat **6:**461–464. doi:10.1214/aos/1176344136.

Shokita S. 1979. The distribution and speciation of the inland water shrimps and prawns from the Ryukyu Islands–II. Bull Coll Sci Univ Ryukyus **28:**193–278. (in Japanese with English summary)

Suzuki H, Tanigawa N, Nagatomo T, Tsuda E. 1993. Distribution of freshwater caridean shrimps and prawns (Atyidae and Palaemonidae) from southern Kyushu and adjacent islands, Kagoshima Prefecture, Japan. Crust Res **22:**55–64. doi:10.18353/crustacea.22.0_55.

Urakawa LS, Kurogi M, Yoshimura K, Hasumi H. 2015. Modeling low salinity waters along the coast around Japan using a high-resolution river discharge dataset. J Oceanogr **71:**715–739. doi:10.1007/s10872-015-0314-4.

Usami Y, Yokota K, Watanabe S. 2008. Longitudinal distributions of freshwater shrimps and prawns (Crustacea, Decapoda, Caridea, Atyidae and Palaemonidae) in Kanto district. Bull Biogeogr Soc Japan **63:**51–62. (in Japanese with English abstract)

Veron JEN, Minchin PR. 1992. Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. Cont Shelf Res **12:**835–857. doi:10.1016/0278-4343(92)90047-N.

Wong JTY. 1989. Abbreviated larval development of *Macrobrachium hainanense* (Parisi, 1919) reared in the laboratory (Decapoda, Caridea, Palaemonidae). Crustaceana **56:**18–30. doi:10.1163/156854089X00752.

Yamahira K, Inoue A, Oishi S, Ideguchi K. 2007. Upstream and downstream variation in demography of the amphidromous shrimp *Caridina leucosticta*. Japan J Benthol **62:**9–16. doi:10.5179/benthos.62.9. (in Japanese with English abstract)

Yatsuya M, Ueno M, Yamashita Y. 2012. Occurrence and distribution of freshwater shrimp in the Isazu and Yura Rivers, Kyoto, western Japan. Plankton Benthos Res **7:**175–187. doi:10.3800/pbr.7.175.

Yatsuya M, Ueno M, Yamashita Y. 2013. Life history of the amphidromous shrimp *Caridina leucosticta* (Decapoda: Caridea: Atyidae) in the Isazu River, Japan. J Crust Biol **33:**488–502. doi:10.1163/1937240X-00002113.

Yokoya Y. 1931. On the metamorphosis of the two Japanese shrimps, *Paratya compressa* and *Leander paucidens*, with reference to the development of their appendages. J Coll Agric Tokyo Imp Univ **11:**75–150.

Supplementary materials

Fig. S1. Changes in the survival rate (circles) and cumulative moulting rate (triangles) to the juvenile stage in relation to days after hatching of *Paratya compressa* larvae. Larvae were reared in water with five salinity levels (4.25, 8.5, 17, 25.5, and 34 ppt) at five different temperatures (mean values): 19.9°C (A), 23.0°C (B), 26.0°C (C), 29.5°C (D), and 33.3°C (E). Larval rearing was terminated when all the surviving larvae had moulted to the juvenile stage. The survival rate was defined as: (number of survivors at the designated days after hatching)/(number of initial larvae) × 100. Cumulative moulting rate to the juvenile stage was defined as: (cumulative number of juveniles at the designated days after hatching)/(number of initial larvae) × 100. (download)

Fig. S2. Changes in the survival rate (circles) and cumulative moulting rate (triangles) to the juvenile stage in relation to days after hatching of *Paratya improvisa* larvae. Larvae were reared in water with five salinity levels (4.25, 8.5, 17, 25.5, and 34 ppt) at five different temperatures (mean values): 20.5°C (A), 23.5°C (B), 26.9°C (C), 29.8°C (D), and 32.9°C (E). Larval rearing was terminated when all the surviving larvae had moulted to the juvenile stage. The survival rate was defined as: (number of survivors at the designated days after hatching)/(number of initial larvae) × 100. Cumulative moulting rate to the juvenile stage was defined as: (cumulative number of juveniles at the designated days after hatching)/(number of initial larvae) × 100. (download)

Table S1. Coefficient estimates with standard errors (SE) for the explanatory variables in the generalised linear model (GLM) or linear model (LM) to evaluate the effects of temperature (T) and salinity (S) on larval survival (alive or not) and duration to reach the juvenile stage (days), and carapace length (mm) of juveniles of *Paratya compressa*. Four models were applied in the binomial- and Poisson-GLM analyses for larval survival and larval duration, respectively, and those in the LM analysis for the carapace length: model 1, $y \sim T + S + T^2 + S^2 + T \times S$; model 2, $y \sim T + S + T^2 + S^2$; model 3, $y \sim T + S + T \times S$; and model 4, $y \sim T + S$. The Bayesian information criterion (BIC) was calculated for each model to select the best model with the minimum BIC. The bold BIC value was the minimum among those of four models. (download)

Table S2. Coefficient estimates with standard errors (SE) for the explanatory variables in the generalised linear model (GLM) or linear model (LM) to evaluate the effects of temperature (T) and salinity (S) on larval survival (alive or not) and duration to reach the juvenile stage (days), and carapace length (mm) of juveniles of *Paratya improvisa*. Four models were applied in the binomial- and Poisson-GLM analyses for larval survival and larval duration, respectively, and those in the LM analysis for the carapace length: model 1, $y \sim T + S + T^2 + S^2 + T \times S$; model 2, $y \sim T + S + T^2 + S^2$; model 3, $y \sim T + S + T \times S$; and model 4, $y \sim T + S$. The Bayesian information criterion (BIC) was calculated for each model to select the best model with the minimum BIC. The bold BIC value was the minimum among those of four models. (download)