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Larval Performance of Amphidromous and Landlocked Atyid Shrimp Species in the Genus *Paratya* under Different Feeding Conditions

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Freshwater shrimps in the family Atyidae exhibit two life history traits: 1) amphidromy, with many small embryos hatching into planktotrophic larvae that develop in the sea, and 2) landlocked, with few large embryos hatching into non-feeding lecithotrophic larvae, or facultative lecithotrophic larvae that develop in freshwater. The lecithotrophy of larvae is considered an adaptation to limited food conditions in the freshwater environment. Furthermore, faster development and settlement behaviours that large larvae exhibit are considered adaptations that allow the larvae to stay in or near parental habitats in fast-flowing streams. We therefore hypothesized that the facultative lecithotrophic larvae of landlocked shrimps might better adapt to limited food conditions as their large body size develops, an adaptation to maintain habitat position in flowing streams, than do planktotrophic larvae of companion amphidromous species developing in the sea. To test this hypothesis, we compared the larval feeding habits and size of two closely related species in the genus *Paratya*: the amphidromous *P. compressa*, with planktotrophic larvae, and the landlocked *P. improvisa*, with facultative lecithotrophic larvae. Larvae were reared by being fed commercially preserved or cultured phytoplankton (*Tetraselmis* sp.) and cultured zooplankton rotifers. *Paratya compressa* larvae did not survive, but *P. improvisa* larvae did develop into the juvenile stage under poor feeding conditions with preserved *Tetraselmis* alone, supporting our hypothesis of the effects of different larval feeding habits in amphidromous and landlocked atyid shrimp species. Hatchlings were larger and larval duration was shorter in *P. improvisa* than in *P. compressa*. *Paratya improvisa* larvae exhibited settlement behaviour beginning with the early zoeal stage. Our results also highlighted the retention strategy by which landlocked *P. improvisa* larvae stay in or near parental habitats.

Key words: Larval development, Larval survival, Feeding habit, Lecithotrophy, Retention strategy.

BACKGROUND

Freshwater shrimps of the family Atyidae are distributed worldwide, except in Antarctica. They 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 play important roles in stream food webs and ecosystems, functioning as primary consumers and food sources for predators (Pringle et al. 1993; Covich and McDowell 1996; Covich et al. 1999; Crowl et al. 2001; Oeding et al. 2020).

Atyid shrimps exhibit one of two life history traits: amphidromous or landlocked (Shokita 1979; Hayashi and Hamano 1984; Bauer 2013). Amphidromous adults

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inhabit and reproduce in freshwater environments, but their larvae require saline waters for successful development (Shokita 1979; Hayashi and Hamano 1984; Nakahara et al. 2005). Amphidromous species spawn many relatively small eggs (Shokita 1979; Hayashi and Hamano 1984; Jalihal et al. 1993; Bauer 2013), and newly hatched larvae (stage 1 zoeae) passively drift from the freshwater environments into the sea (Ideguchi et al. 2000 2007; Hamano et al. 2005). Larvae develop through longer periods of complex zoeal stages in the brackish water of estuaries and coastal bays or in the open sea (Hayashi and Hamamo 1984; Jalihal et al. 1993; Ideguchi et al. 2007; Yatsuya et al. 2013). After recruitment to the mouth of a coastal river or stream, juveniles migrate up into the adult freshwater habitat (Hamano and Hayashi 1992; Hamano et al. 2005; Bauer 2013; Yatsuya et al. 2013).

On the contrary, landlocked species complete their entire lifecycle within freshwater habitats and exhibit intra- and interspecific variabilities in their reproductive traits (Shokita 1979; Hancock 1998; Hancock et al. 1998; Bauer 2013). In a few landlocked species with small eggs, extended larval development—as in the case of amphidromous shrimps—occurs in freshwater habitats like large lakes (Bauer 2013). In general, however, landlocked shrimps spawn a relatively small number of large eggs with considerable amounts of yolk. These produce morphologically advanced hatchlings, resulting in a shortened larval development period with few successive zoeal stages (abbreviated larval development) before moulting into the juvenile stage (*sensu* Møller et al. 2020), or directly producing juveniles (direct larval development) (Shokita 1979; Hayashi and Hamano 1984; Jalihal et al. 1993; 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 marine ancestral species through freshwater amphidromous to landlocked species (Bauer 2013). It has been suggested that insufficient, unpredictable, or seasonally short production of food for larvae in freshwater environments (Shokita 1979; Anger 2001 2006; Bauer 2013) are the major driving forces behind the landlocked life history trait associated with few and large eggs. Larger embryos produce non-feeding lecithotrophic larvae, which thoroughly rely on yolk left over from the embryo, or facultative lecithotrophic larvae, which rely on endogenous yolk and exogenous feeding (Jalihal et al. 1993; Anger 2001; Kawamura and Akiyama 2010). Besides larval nutritional conditions, faster development and settlement behaviours that large larvae exhibit are considered adaptations that allow the larvae to stay in or near parental habitats in fast-flowing streams (Shokita 1979; Mashiko 1982 1990; Dudgeon 1985; Wong 1989; Hancock 1998; Hancock et al. 1998). We therefore hypothesized that the facultative lecithotrophic larvae of landlocked shrimps adapt better to limited food conditions while developing their large body size—an adaptation to maintain habitat position in flowing streams—than do planktotrophic larvae of companion amphidromous species developing in the sea. However, to the best of our knowledge, no studies have compared the larval feeding habits and size between closely related amphidromous and landlocked shrimp species.

In the present study, we tested the hypothesis that feeding habits and size affect the larval performance of two species in the genus *Paratya* Miers 1882: the amphidromous *P. compressa* (De Haan 1844) and the landlocked *P. improvisa* Kemp 1917. We conducted larval culture experiments under different feeding conditions. Our results highlight the different larval feeding habits and sizes, as well as the adaptive value of these traits in two related species, one with amphidromous and the other with landlocked atyid larvae.

MATERIALS AND METHODS

Test species

Paratya compressa and *P. improvisa* are closely related species of atyid shrimps (Ikeda 1999; Page et al. 2005). *Paratya compressa* is an amphidromous species with many small eggs (Kawamura and Akiyama 2010). It inhabits lower and middle reaches with boulders in south-western Japan (Shokita 1979; Hamano and Hayashi 1992; Suzuki et al. 1993; Ikeda 1999; Usami et al. 2008; Saito et al. 2012). *Paratya improvisa* is landlocked with few, relatively large eggs (Kawamura and Akiyama 2010). It inhabits lentic systems of the lower to upper reaches in north-eastern Japan (Ikeda 1999; Imai 2006; Yatsuya et al. 2012). Kawamura and Akiyama (2010) reported that both *P. compressa* and *P. improvisa* larvae undergo eight zoeal stages before moulting into the juvenile stage. *Paratya compressa* larvae are shown to be planktotrophic, whereas *P. improvisa* larvae can moult to stage 3 zoeae without food (*i.e.*, facultative lecithotrophy) and have a shorter larval developmental duration than do *P. compressa* larvae.

Larval source

Culture experiments were conducted in a laboratory at the Tokyo University of Marine Science and Technology, Tokyo, Japan in 2017 and 2018. Wild mature female and male test shrimps were captured from April to May using scoop nets at the following locations in Chiba Prefecture, Japan: *P. compressa*, Banda River (34°58'N, 139°46'E); and *P. improvisa*, Yoro River (35°21'N, 140°08'E).

Females were cultured with males in aerated aquaria (23 litres) under natural photoperiod conditions (20–30 shrimps per tank, unknown sex ratio). Aquarium temperature was maintained at approximately 23°C using a heater and an air conditioner in the laboratory. This falls within the range of summer temperatures during the reproductive season of atyid shrimps in their natural habitat (Imai 2006; Saito et al. 2012; Yatsuya et al. 2012). Artificial diets for ornamental shrimps or fish were provided daily. Half of the rearing water was replaced with fresh water every three days. Ovigerous females were transferred and individually contained in beakers (1 litre). Ovigerous females were fed an artificial diet each day. 200 ml of rearing water was exchanged for fresh water daily.

Newly hatched larvae (stage 1 zoeae) from two brood females of each species were used for the larval culture experiments. The larval hatching date of each species-brood was as follows: *P. compressa* brood 1, August 31, 2017; *P. compressa* brood 2, May 12, 2018; *P. improvisa* brood 1, July 14, 2017; and *P. improvisa* brood 2, July 23, 2017. The 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 10 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 image analysing system (Nikon Digital Sight and NIS-Elements software, Nikon Corp., Tokyo, Japan).

Feeding conditions

We previously conducted experiments to examine the dietary effects of euryhaline phytoplankton *Tetraselmis* sp. (cell diameter, ~10–12 μm) and euryhaline zooplankton, rotifers in the *Brachionus plicatilis* species complex (small-morphotype; body size, ~0.1–0.2 mm in lorica length) on the survival, duration, and growth of larvae of four amphidromous atyid shrimp species in the genus *Caridina* H. Milne-Edwards 1837. These were *C. leucosticta* Stimpson 1860, *C. multidentata* Stimpson 1860, *C. serratirostris* De Man 1892, and *C. typus* H. Milne-Edwards 1837 (Hamasaki et al. 2020). In these experiments, we used a commercial, condensed paste of *Tetraselmis* sp. stored at 4°C (preserved *Tetraselmis*) (Tetraselmis 3600®, Reed Mariculture Inc., Campbell, CA, USA) and live *Tetraselmis* sp. cultured in our laboratory (cultured *Tetraselmis*). *Tetraselmis* sp. is a green unicellular alga with four distinct flagella. Algal cells of cultured *Tetraselmis* can move around freely in seawater, whereas those of preserved *Tetraselmis* were intact but nonviable. In the present study, larvae of *Paratya* species were reared under five different feeding conditions with phytoplankton, rotifers, and their combinations as follows: 1) preserved *Tetraselmis* (PT), 2) cultured *Tetraselmis* (CT), 3) rotifers (R), 4) preserved *Tetraselmis* and rotifers (PTR), and 5) cultured *Tetraselmis* and rotifers (CTR). Our previous experiments revealed that cultured *Tetraselmis* and rotifers successfully sustain the larval development into the juvenile stage in *Caridina* species under CT and CTR conditions, but the nutritional conditions of their larvae were considered poor when they were fed preserved *Tetraselmis* and/or rotifers under the PT, R, and PTR conditions (Hamasaki et al. 2020).

Tetraselmis sp. were cultured in glass containers with seawater (salinity, 34 ppt; 24–26°C) supplemented with fertilizers for algal culture (KW21, Daiichi Seimo Co. Ltd., Kumamoto, Japan) under constant illumination. The rotifers were cultured in plastic containers with seawater (salinity, 24 ppt; 23–24°C) supplied with commercial, condensed freshwater phytoplankton, *Chlorella vulgaris* (Super Chlorella V12, Chlorella Industry, Tokyo, Japan).

Larval culture

Thirty newly hatched larvae (stage 1 zoeae) were used for each feeding condition in each species brood. Larvae were housed individually in the wells of six-well cell culture plates, each well of which contained 8 ml of artificial saline water. The feeding density and larval rearing environments followed our previous study of cultured larvae of *Caridina* species (Hamasaki et al. 2020): *Tetraselmis* sp., 1×10^5 cells ml^{-1}; rotifers, 20 individuals ml^{-1}; salinity, 17 ppt; and temperature, 26°C. Although *P. improvisa* is a landlocked shrimp, its larvae can develop in saline water and live longer in saline water of 8.5 ppt and 17 ppt than in water of other salinity levels (0, 25.5, and 34 ppt) under starvation conditions (Kawamura and Akiyama 2010). Larval rearing temperature (26°C) is in the range of the summer sea surface temperatures along the Pacific coasts of Japan (Japan Meteorological Agency 2020) or in a natural pond (Imai 2006), where larvae of *P.*

compressa and *P. improvisa* may develop, respectively. The salinity of larval rearing water was regulated using artificial seawater salt (Sealife, Marinetech Co. Ltd., Tokyo, Japan). Larval culture plates were set in temperature-controlled incubation chambers under a photoperiod cycle of 14 h light and 10 h dark.

Each morning, glass pipettes were used to transfer larvae to clean culture wells containing fresh saline water and food, and the number of live and dead larvae were recorded under a stereomicroscope. Each larva was also checked for the presence of an exuvia. Larval rearing was terminated when all surviving larvae had moulted into the juvenile stage. We observed later stage larvae under a stereomicroscope and determined whether they moulted into the juvenile stage based on the morphologies of their first and second antennae, as described by Kawamura and Akiyama (2010). The final survival rate of larvae was defined for each feeding condition in each species-brood as: (number of larvae that moulted into the juvenile stage)/(number of initial larvae) × 100.

Juvenile survivors of each species-brood were fixed and preserved in the same way as 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).

Statistical analysis

Statistical analyses were performed using R statistical software (R4.0.2; R Core Team 2020) with a 5% significance level. Survival curves were compared among different feeding conditions in each species with a log-rank test stratified by the brood identity using the *survdiff* function implemented in the survival package (Therneau 2020). The effects of different feeding conditions (categorical explanatory variable) on the number of days required to moult into the juvenile stage (*i.e.*, larval duration) (response variable) was evaluated in each species using a generalized linear mixed-effects model (GLMM) with a Poisson distribution, taking into account the inter-brood variability (Zuur et al. 2009). A linear mixed-effects model (LMM) was also employed to compare the larval growth (*i.e.*, the carapace length of juveniles) (response variable) among different feeding conditions (categorical explanatory variable) in each species. In these analyses, brood identity was included as the random intercept effect. The GLMM and LMM analyses were performed using the *glmer* function (log link) and *lmer* function (identical link) in the lme4 package (Bate et al. 2015), respectively. The statistical significance of the explanatory variable was evaluated with the type II Wald chi-square test and Type II Wald *F* test with Kenward-Roger *d.f.* in the GLMM and LMM analyses, respectively, using the *Anova* function in the car package (Fox and Weisberg 2011). Differences in larval duration and carapace length between feeding conditions in each species were tested with Tukey's method using the *glht* function in the multcomp package (Hothorn et al. 2008).

The difference between the numbers of moults during the larval stage among different feeding conditions was not statistically tested because some exuviae of larvae appeared to be missed during the culture operations (see the RESULTS section).

RESULTS

The carapace length of stage 1 zoeae (mean ± standard deviation) of *P. compressa* broods 1 and 2 was 0.277 ± 0.030 mm and 0.321 ± 0.030 mm, respectively. In *P. compressa*, we observed a significant difference in larval survival to the juvenile stage between different feeding conditions ($\chi^2 = 185.6$, *d.f.* = 4, $P < 0.0001$) (Fig. 1A, B). When larvae were supplied with preserved *Tetraselmis* alone, brood 1 larvae never moulted and 23.3% of brood 2 larvae moulted once. All larvae from both broods died within 16 days of hatching (Fig. 1A, B; see supplementary Table S1 for survival and moulting data on larvae that had died prior to moulting into the juvenile stage). Larvae survived to the juvenile stage when they were fed cultured *Tetraselmis* and/or rotifers, and preserved *Tetraselmis* with rotifers under the CT, R, PTR, and CTR conditions. Larval survival rates began to vary among feeding conditions between 6 and 13 days after hatching (Fig. 1A, B), and the final survival rate was higher in the CTR group (90.0%) than in other groups (40.0–60.0%) in brood 1. In brood 2, the final survival rate was higher in the CT and CTR groups (60.0–66.7%) than in other groups (3.3–10%) (Fig. 2A; see supplementary Table S2 for survival and development data on larvae that survived to the juvenile stage). Feeding conditions significantly influenced the larval phase duration (Fig. 2B) ($\chi^2 = 104.4$, *d.f.* = 3, $P < 0.0001$) and carapace length of juveniles (Fig. 2C) ($F_{3,\ 110.5} = 3.70$, $P = 0.0140$). Larval development and growth tended to be enhanced in the CT and CTR groups.

The carapace length of stage 1 zoeae of *P. improvisa* broods 1 and 2 was 0.626 ± 0.050 mm and 0.603 ± 0.023 mm, respectively. Larvae of *P. improvisa* tended to stay on the bottom of the rearing container beginning with the early zoeal stage. In *P. improvisa*, survival curves were significantly different between feeding conditions ($\chi^2 = 134.8$, *d.f.* = 4, $P < 0.0001$) (Fig. 1C, D). Larvae survived to the juvenile stage in all feeding groups except for brood 2 larvae in the PT group, which moulted 1–4 times but died within 13 days of hatching (Fig. 1C, D; Table S1). Larval survival was substantially improved in the CT, PTR, and CTR groups, as shown by the higher final survival rates (93.3–100%) compared to other groups (16.7–53.3%) (Fig. 2A; Table S2). Significant differences were found in larval duration (Fig. 2B) (χ^2 = 95.5, *d.f.* = 3, P < 0.0001) and the carapace length of juveniles (Fig. 2C) ($F_{4,\ 196.4}$ = 152.6, P < 0.0001) for different feeding conditions. Larval development and growth tended to be improved in groups with higher survival rates, particularly the CT and CTR groups.

The number of times that larvae moulted before reaching the juvenile stage varied from 3–13 in *P. compressa* and 2–6 in *P. improvisa* (Table S2), and the minimum moulting frequencies were lower than the number of zoeal stages (eight) reported for these species (Kawamura and Akiyama 2010), suggesting that some exuviae were missed during the culture operations.

DISCUSSION

Our larval culture experiments demonstrated that feeding conditions significantly affected larval survival, duration, and growth for the two *Paratya* species with different life history traits, namely amphidromous *P. compressa* and landlocked *P. improvisa* (Figs. 1 and 2). The larval development and growth tended to be enhanced under the feeding conditions that resulted in higher survival rates in both species. Although larval survival among the different feeding conditions varied between the two broods of *P. compressa*, overall, the final survival rates were high when larvae were fed with cultured *Tetraselmis* and cultured *Tetraselmis* with rotifers. Larvae did not survive to reach the juvenile stage when fed preserved *Tetraselmis* alone (Table S1). In *P. improvisa*, the final larval survival rates were high when larvae were fed cultured *Tetraselmis*, preserved *Tetraselmis* with rotifers, and cultured *Tetraselmis* with rotifers compared to those of larvae fed solely on rotifers. A small proportion of larvae (brood 1) survived and developed into the juvenile stage, even when they were fed preserved *Tetraselmis* alone. Thus, the survival and development of *P. compressa* and *P. improvisa* larvae differed among the various feeding conditions.

In our larval culture experiments, early larvae of both *P. compressa* and *P. improvisa* appeared to ingest both preserved and cultured *Tetraselmis* because green microalgal substances were observed in the digestive tracts of the larvae under a stereomicroscope. Nevertheless, when larvae were fed preserved *Tetraselmis* alone, the only larvae that survived long enough to reach the juvenile stage was the brood 1 larvae of *P. improvisa*. We established that larval development and survival depend on diet. As such, it is interesting to note that different nutritional components may play key roles. For instance, the fatty acid composition and amount of fatty acid in live food significantly affect larval survival, growth, and development in aquatic

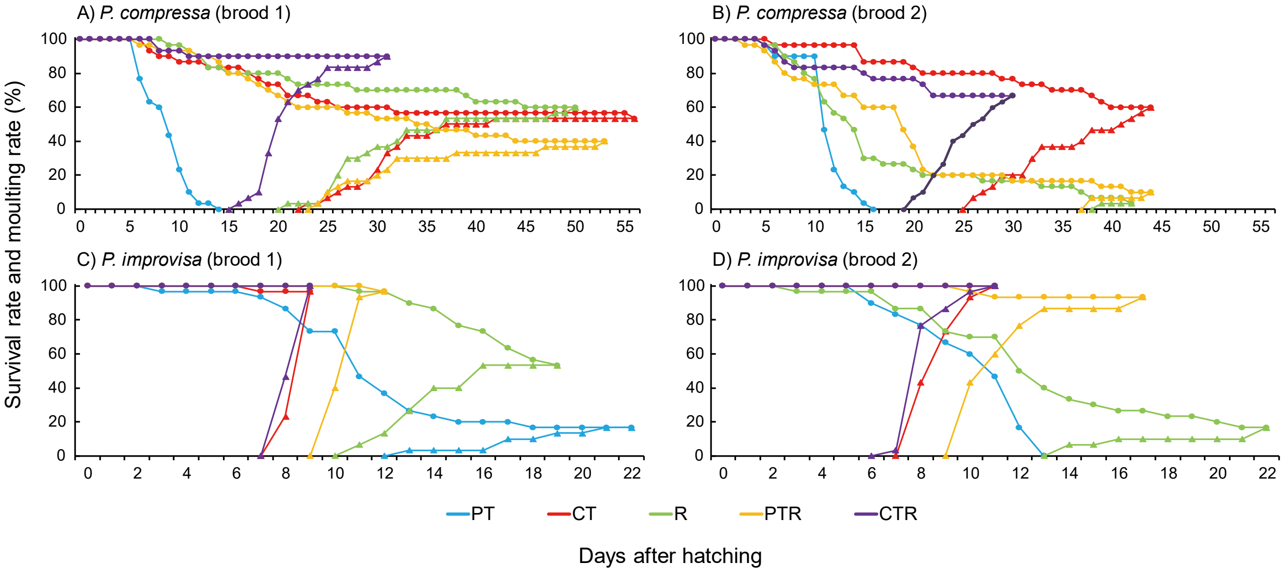

Fig. 1. Changes in the survival rate (circle symbols) and cumulative moulting rate (triangle symbols) into the juvenile stage in relation to days after hatching of the larvae hatched from two different brooding females in two atyid shrimp species, *Paratya compressa* (A, B) and *P. improvisa* (C, D). Larvae were reared on five different diet combinations of phytoplankton (*Tetraselmis* sp.) and zooplankton rotifers: preserved *Tetraselmis* (PT), cultured *Tetraselmis* (CT), rotifers (R), preserved *Tetraselmis* with rotifers (PTR), and cultured *Tetraselmis* with rotifers (CTR). Larval rearing was terminated when all surviving larvae had moulted into the juvenile stage.

organisms, including decapod crustaceans (Montaini et al. 1995; Anger 2001; Tocher 2010). The preserved *Tetraselmis suecica* has been shown to maintain its fatty acid profile when stored at 4°C (Montaini et al. 1995).

Feeding behaviour is another factor that may affect larval nutritional intake. Atyid shrimp larvae ingest phytoplankton via suspension feeding (Nakahara et al. 2007). Consequently, the voluntary movement of live

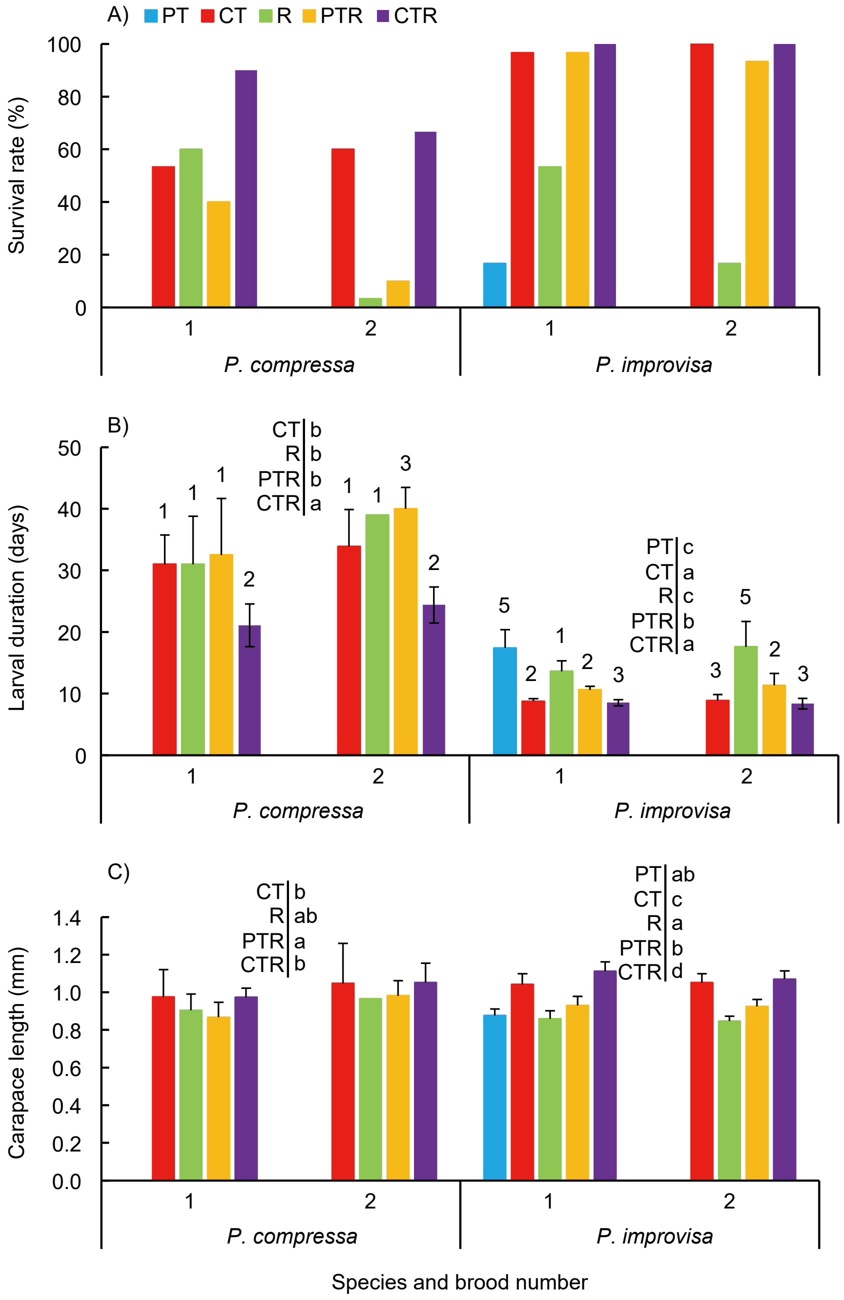

Fig. 2. Survival rate from hatching to the juvenile stage (A), number of days required to moult into the juvenile stage (larval duration) (B), and carapace length of juveniles (C) in the larvae of two atyid shrimp species, *Paratya compressa* and *P. improvisa*. Larvae were reared on five different diet combinations of phytoplankton (*Tetraselmis* sp.) and zooplankton rotifers: preserved *Tetraselmis* (PT), cultured *Tetraselmis* (CT), rotifers (R), preserved *Tetraselmis* with rotifers (PTR), and cultured *Tetraselmis* with rotifers (CTR). Larval rearing was terminated when all surviving larvae had moulted into the juvenile stage. Bars and vertical lines in panels (B) and (C) indicate mean and standard deviation values, respectively. Numbers of individuals are shown above the bars for each species brood in panel (B). Differences in larval duration and carapace length between feeding conditions in each species ($P < 0.05$) are indicated by different lowercase letters in the tables following the feeding conditions in panels (B) and (C), respectively.

algal cells of cultured *Tetraselmis* might enhance the efficiency of suspension feeding, whereas the nonviable cells of preserved *Tetraselmis* might substantially lower the larval suspension feeding efficiency, resulting in larval nutritional deficiency.

Kawamura and Akiyama (2010) examined the starvation tolerance of newly hatched larvae of *P. compressa* and *P. improvisa* under different temperature (19, 21, 23, 25, 27, and 29°C) and salinity (0, 8.5, 17.0, 25.5, and 34.0 ppt) combinations. They reported that, under starvation conditions at 25–27°C and salinity of 17 ppt, which are equivalent to the larval rearing conditions in the present study, mean survival time was ~7–9 days in *P. compressa* and ~6 days in *P. improvisa*. They also showed that *P. compressa* larvae never moulted, whereas 100% and 84–92% of *P. improvisa* larvae moulted once and twice, respectively. In our larval culture experiments, under the feeding condition with preserved *Tetraselmis* alone, the mean survival time of larvae that died was ~9–11 days in *P. compressa* and ~11–13 days in *P. improvisa*. In *P. compressa*, brood 1 larvae never moulted, and a small proportion of brood 2 larvae moulted once. *Paratya improvisa* larvae, however, moulted 1–3 times (mean, 2.0 times) in brood 1 and 1–4 times (mean, 2.0 times) in brood 2 (Table S1). Consequently, the relative survival time of fed larvae to that of unfed larvae was more prolonged in *P. improvisa* than in *P. compressa* under the limited nutritional condition with preserved *Tetraselmis* alone. This is likely due to the facultative lecithotrophy of *P. improvisa* larvae.

Larval survival rates of *P. compressa* linearly decreased from about 6–11 days after hatching and larvae did not survive to the juvenile stage under feeding with preserved *Tetraselmis* alone. Supplementing rotifers with preserved *Tetraselmis*, however, sustained larval survival and development into the juvenile stage (Fig. 1). Larval survival curves were similar under the feeding conditions with rotifers alone and with preserved *Tetraselmis* and rotifers, particularly in brood 2 (Fig. 1). These results suggest that *P. compressa* larvae might be able to ingest rotifers from an early stage. Additionally, feeding cultured *Tetraselmis* with rotifers improved larval survival and developmental rate, particularly from about 13 days after hatching (brood 1), compared to feeding cultured *Tetraselmis* alone (Fig. 1). Our results suggest that ingesting larger rotifers (~0.1–0.2 mm) coupled with cultured *Tetraselmis* (~10–12 µm) might enhance the larval feeding efficiency and thereby improve the nutritional condition of larvae from the middle stage, resulting in a higher survival rate and faster development of larvae (Fig. 2).

Given that feeding rotifers alone sustained larval survival into the juvenile stage but preserved *Tetraselmis* alone resulted in a decrease in survival from about 6 days after hatching (Fig. 1), we deduced that *P. improvisa* larvae are likely able to digest rotifers from an early stage. The dietary effects of preserved *Tetraselmis* and rotifers on larval performance were significantly improved when they were given to the larvae in combination rather than alone (Fig. 2). Atyid shrimp larvae can ingest detritus (Hayashi and Hamano 1984; Hancock 1998) and rotifers can be cultured and reproduced when fed *Tetraselmis* sp. (Hagiwara et al. 2007). Detritus (*i.e.*, faeces) generated by rotifers that were fed preserved *Tetraselmis* may make a better food source for *P. improvisa* larvae. Taken together, this suggests that *P. improvisa* larvae could survive into the juvenile stage under the poor feeding conditions limited to preserved *Tetraselmis* and detritus derived from rotifers fed on preserved *Tetraselmis*. This supports our hypothesis that facultative lecithotrophic larvae of landlocked shrimps might better adapt to limited food conditions than equivalent larvae of companion amphidromous species.

Hamasaki et al. (2020) conducted larval culture experiments to determine the larval ecology of four amphidromous atyid shrimps, *C. leucosticta*, *C. multidentata*, *C. serratirostris*, and *C. typus*. They reared larvae under the same five feeding conditions employed in the present study. Larvae of *C. serratirostris* died because they were trapped by the surface tension of the water during moulting. In the three remaining species, feeding with preserved *Tetraselmis*, rotifers, and a combination of the two did not sustain the larval survival or development into the juvenile stage. Larvae could, however, survive to become juveniles when they were fed cultured *Tetraselmis* alone and cultured *Tetraselmis* and rotifers. Hamasaki et al. (2020) suggested that *C. leucosticta* larvae may have adapted to develop in eutrophic brackish environments with substantial phytoplankton biomass because they moulted into juveniles with high survival rates by being fed only cultured *Tetraselmis*. *Caridina* species thus behaved differently from the *P. compressa* larvae used in this study, as evidenced by the *P. compressa* larvae's ability to develop into the juvenile stage under the poor condition of being fed rotifers alone and being fed preserved *Tetraselmis* and rotifers (Fig. 1). *Paratya compressa* larvae are able to develop in oligotrophic environments in coastal and offshore sea, thus enabling wide sea dispersion. Phylogeographic studies are required to determine the extent of *P. compressa* larvae's aquatic distribution.

Direct larval development or abbreviated larval development into the juvenile stage of landlocked freshwater shrimps have been considered adaptations to stay in or near parental habitats in fast-flowing streams (Shokita 1979; Mashiko 1982 1990; Dudgeon 1985; Wong 1989). Morphologically advanced larvae may have the ability to grasp trailing vegetation and roots and thereby avoid being swept away by fast-flowing water (Dudgeon 1985). Hancock (1998) examined the relationship between egg size and larval development of *Paratya australiensis* Kemp 1917 collected from headwater streams of the Conondale Rage, Queensland, Australia. Shrimps with large eggs and small eggs were obtained from upper and lower altitude sites, respectively. He reported that larval size depends on egg size. Large larvae from large eggs developed faster than did those from small eggs, but large and small larvae had similar larval developmental pathways into the juvenile stage. Hancock (1998) and Hancock et al. (1998) suggested that the production of larger, more rapidly developing larvae at upper altitude sites may reduce the chance of larvae being swept into downstream sites, from where it would be difficult to repopulate the source population. The body size (carapace length) of stage 1 zoeae was larger in *P. improvisa* (mean, 0.603–0.626 mm) than in *P. compressa* (mean, 0.277–0.321 mm), but juvenile body size was similar in *P. improvisa* (mean, 0.847–1.112 mm) and *P. compressa* (mean, 0.868–1.048 mm), and larval duration was shorter in *P. improvisa* (mean, 8–18 days) than in *P. compressa* (mean, 21–40 days) (Fig. 2; Table S2). Larval developmental stages are not shortened in *P. improvisa* because they have eight zoeal stages, similar to amphidromous *P. compressa* (Kawamura and Akiyama 2010). Larvae of *P. improvisa* tended to exhibit settlement behaviour in the rearing container beginning with the early zoeal stage. Therefore, faster development and behavioural characteristics of *P. improvisa* larvae are considered to be adaptations that increase the chance of maintaining the larvae's position in or near parental habitats in lower to upper reaches of various lentic systems (Ikeda 1999; Imai 2006; Yatsuya et al. 2012).

CONCLUSIONS

Our larval culture experiments support the hypothesis that facultative lecithotrophic larvae of landlocked shrimps might adapt better to limited food conditions than do planktotrophic larvae of companion amphidromous species. Facultative lecithotrophic larvae of landlocked *P. improvisa* could survive and develop into the juvenile stage under poor feeding conditions that are not suitable for the survival and development of planktotrophic larvae of amphidromous *P. compressa*. The present study thus provides empirical data that suggest that limited food conditions are a major selective force influencing landlocked life history traits with few and large eggs (*i.e.*, larvae). Such limitations include insufficient, unpredictable, or seasonally short production of food in freshwater habitats (Shokita 1979; Anger 2001 2006; Bauer 2013). Our results and observations further highlight strategies that landlocked *P. improvisa* larvae use to stay in or near parental habitats—*i.e.*, fast development and behavioural characteristics.

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

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Supplementary Materials

Table S1. Moulting incidences of larvae that died in two atyid shrimp species in the genus *Paratya* under different feeding conditions. PT, preserved *Tetraselmis*; CT, cultured *Tetraselmis*; R, rotifers; PTR, preserved *Tetraselmis* and rotifers; CTR, cultured *Tetraselmis* and rotifers. Number of moults was calculated for larvae that moulted. (download)

Table S2. Larval survival, duration, and growth of two atyid shrimp species in the genus *Paratya* under different feeding conditions. PT, preserved *Tetraselmis*; CT, cultured *Tetraselmis*; R, rotifers; PTR, preserved *Tetraselmis* and rotifers; CTR, cultured *Tetraselmis* and rotifers. (download)