

## Effects of temperature and salinity on larval survival, duration and growth of the atyid shrimp *Caridina serratiostris* under laboratory conditions

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### Abstract

Temperature and salinity are the most important environmental factors that affect the survival, duration and growth of decapod crustacean larvae. 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 freshwater shrimps. We examined the effects of temperature and salinity on larval performance of the amphidromous atyid shrimp *Caridina serratiostris* to infer larval dispersal strategy in the sea. Larvae were reared under 16 combinations of four different temperatures (20, 23, 26 and 29°C) and salinity levels (8.5, 17, 25.5 and 34 ppt). Temperature and salinity significantly affected larval performance, and larvae survived to the juvenile stage at 20–29°C and 17–34 ppt, with higher survival rates at 20–26°C and 25.5–34 ppt. *C. serratiostris* larvae may disperse broadly under the high salinity condition of the open sea (34 ppt), but their ocean dispersal may be restricted under high seawater temperature conditions (~30°C) during the summer season.

**Keywords:** amphidromous shrimp; larval dispersal, larval culture; environmental adaptation; Decapoda; Caridea

### Introduction

Freshwater shrimp *Caridina serratiostris* De Man, 1892 (Decapoda: Caridina: Atyidae) inhabits the lower reaches of rivers throughout the Indo-Pacific (Shokita 1979; Cai and Shokita 2006; Page et al. 2005; Saito et al. 2012; Yatsuya et al. 2012; Hoarau 2018). *C. serratiostris* exhibits an amphidromous life cycle where the larvae require saline water for successful development (Nakahara et al. 2005).

Newly hatched larvae (stage 1 zoeae) of amphidromous shrimps drift passively from freshwater environments to the sea, and juveniles migrate up to the adult freshwater habitat after completing their larval life in the sea (Hamano et al. 2005; Bauer, 2013). Populations of the amphidromous freshwater shrimp are thus connected through marine larval dispersal

(Shokita 1979; Bauer 2013; Fujita et al. 2016).

Therefore, knowledge of the environmental factors affecting larval survival, duration and growth is crucial for a better understanding of population connectivity through marine larval dispersal in the amphidromous shrimp species.

Temperature and salinity are the most important environmental factors affecting the larval performance of decapod crustaceans (Anger 2001, 2003), which include the atyid shrimp species (Hamasaki et al. 2021; Kondo et al. 2021). However, little is known about the larval performance of *C. serratiostris* under different temperature and salinity conditions. To date, a laboratory culture using *C. serratiostris* larvae has been conducted under two salinity levels only (0 and 25.5 ppt) and at temperatures of 25–27°C (Nakahara et al. 2005).

The aim of the present study was to evaluate the effects of temperature and salinity on larval survival, duration and growth of *C. serratiostris*. We discuss the larval dispersal strategy of *C. serratiostris* by comparing the larval performance of amphidromous atyid shrimp species under different temperature and salinity conditions.

## Materials and Methods

### Larval source

Culture experiments were conducted in a laboratory at Tokyo University of Marine Science and Technology, Tokyo, Japan. Wild mature female and male shrimps were captured using scoop nets in the Banda River (34°58'N, 139°46'E), Chiba Prefecture, Japan, between July and September 2019.

The shrimps were cultured in aerated aquaria (23 litres) (30–40 shrimps per tank, unknown sex ratio) under natural photoperiod conditions at approximately 23°C, according to the method detailed in our previous study (Hamasaki et al. 2020a). The larval culture experiment was conducted twice (experiments 1 and 2) using newly hatched larvae (stage 1 zoeae) from single females.

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 from each brood was measured from the posterior margin of the sessile eyes to the central posterior margin of the carapace (Nakahara et al. 2007a) 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 larval hatching date and carapace length of the stage 1 zoeae from each brood were

as follows: brood 1, August 21,  $0.269 \pm 0.012$  mm; brood 2, September 20,  $0.266 \pm 0.015$  mm.

### Experimental temperature and salinity conditions

We evaluated the larval performance of *C. serratiostris* under 16 combinations of four different temperatures (20, 23, 26 and 29°C) and salinity levels (8.5, 17, 25.5 and 34 ppt). Temperature levels were selected according to the normal sea surface temperature (~20–30°C) around the Japanese coastal area (Japan Meteorological Agency 2021) during the reproductive seasons of *C. serratiostris* [March to November off Okinawajima Island (26°45'N, 128°12'E) of the Ryukyu Archipelago (Shokita 1979); and June to October off the Boso Peninsula (34°58'N, 139°46'E) of mainland Japan (Hamasaki et al. unpublished data)]. Salinity levels were set assuming salinity profiles from river mouths to the open sea where the atyid larvae of the genus *Caridina* may develop (Ideguchi et al. 2000; Yatsuya et al. 2013; Urakawa et al. 2015).

Larval culture temperatures were adjusted at designated levels ( $\pm 0.5^\circ\text{C}$ ) using temperature-controlled baths in an experimental room with a 14 h light and 10 h dark photoperiod cycle. Larval rearing water was prepared with different salinities using dechlorinated tap water and artificial seawater salts (Sealife, Marinotech Co. Ltd., Tokyo, Japan). Rearing temperatures (mean  $\pm$  standard deviation), recorded once in the morning during the larval culture periods, were as follows: experiment 1:  $20.1 \pm 0.2^\circ\text{C}$ ,  $23.1 \pm 0.3^\circ\text{C}$ ,  $26.0 \pm 0.4^\circ\text{C}$ , and  $28.9 \pm 0.4^\circ\text{C}$ ; and experiment 2:  $20.1 \pm 0.2^\circ\text{C}$ ,  $23.1 \pm 0.2^\circ\text{C}$ ,  $26.0 \pm 0.3^\circ\text{C}$ , and  $29.0 \pm 0.3^\circ\text{C}$ . For convenience, these larval rearing temperatures were referred to as 20, 23, 26 and 29°C, respectively.

### Laval culture method

Stage 1 zoeae were stocked in 100 ml white plastic beakers (10 individuals per beaker) containing 100 ml seawater at designated salinity levels, and the beakers were placed in temperature-controlled baths. Three replicates were prepared for each temperature-salinity combination (a total of 48 beakers in each experiment). The opening of each beaker was wrapped with plastic cling film to prevent evaporation of the larval rearing water. Aeration was not provided for the culture beakers.

Larvae were fed euryhaline phytoplankton *Tetraselmis* sp. at  $1 \times 10^5$  cells  $\text{ml}^{-1}$  in each experiment. In experiment 2, euryhaline zooplankton, the rotifer *Brachionus plicatilis* species complex (small-morphotype), was also given to larvae at 20 individuals  $\text{ml}^{-1}$ ; this was added once more than half of the surviving larvae had moulted to the fourth zoeal stage. These plankton organisms are effective food for culturing the larvae of atyid shrimps (Nakahara et al. 2005; Hamasaki et al. 2020a, b). *Tetraselmis* sp. and the rotifers were cultured according to the methods detailed in our previous studies (Hamasaki et al. 2020a, b).

Each morning, the larvae were transferred to clean culture beakers with fresh saline water and food using a glass pipette, and the numbers of live and dead larvae were recorded. 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 had moulted to the juvenile stage based on their behaviour as well as on their external morphology. Larvae were considered as having reached the juvenile stage when they were able to settle steadily on the bottom of a rearing container using the endopods of their pereopods and to swim in the normal

manner, using their pleopods for propulsion, while showing the morphological characteristics that equalled or advanced those described for the first juvenile stage of *C. serratirostris* (Nakahara et al. 2007a). The final survival rate of larvae was defined for each culture beaker as: (number of larvae that moulted into the juvenile stage) / (number of initial larvae)  $\times 100$ .

The number of zoeal stages is reported as 9–10, and mainly 9 for *C. serratirostris* (Nakahara et al. 2007a), and it is easy to distinguish the stages of the zoeae with the naked eye until the larvae moult to the fourth zoeal stage because of distinct morphological changes (Nakahara et al. 2007a, b). However, 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). Therefore, the moulting events were not considered as larval performance in the present study.

Surviving juveniles were fixed and preserved similarly to the stage 1 zoea specimens, and the carapace length was measured from the posterior margin of the orbit to the central posterior margin of the carapace (Nakahara et al. 2007a). In both experiments 1 and 2, one specimen reared at 23°C–25.5 ppt was not measured due to damage to their carapaces.

### Statistical analysis

Statistical analyses were performed using R statistical software (R4.1.1; R Core Team 2021) at a 5 % significance level. We used a generalised linear model (GLM) with a binomial distribution to evaluate the effects of temperature and salinity levels (categorical explanatory variables) on the final survival rate of the larvae (response variable). The influences of temperature and salinity levels (categorical explanatory variables)

on the larval duration, that is, the number of days required to moult into the juvenile stage, and the larval growth, that is, the carapace length of the juveniles (the response variables) were also evaluated using a generalised linear mixed-effects model (GLMM) with a Poisson distribution and a linear mixed-effects model (LMM), respectively. In the GLMM and LMM analyses, culture beaker identity was included as a random intercept effect to avoid pseudo-replication (Zuur et al. 2009).

The binomial GLM analyses were performed using the `glm` function (logit link), and the statistical significance of the explanatory variables was evaluated with a likelihood ratio test using the `Anova` function (Type II) implemented in the `car` package (Fox and Weisberg 2019). The Poisson GLMM and LMM analyses were conducted using the `glmer` (log

link) and `lmer` functions implemented in the `lme4` package (Bates et al. 2015), respectively, and the statistical significance of the explanatory variables in the Poisson GLMM and LMM analyses was evaluated by a Wald- $\chi^2$  test and a Wald F-test with Kenward-Roger df, respectively, using the `Anova` function (Type II).

## Results

### Larval survival

Temperature (T) and salinity (S) significantly affected larval survival in both experiments (experiment 1:  $n = 48$ : T,  $\chi^2 = 22.81$ ,  $df = 3$ ,  $p < 0.0001$ ; S,  $\chi^2 = 60.30$ ,  $df = 3$ ,  $p < 0.0001$ ; experiment 2:  $n = 48$ : T,  $\chi^2 = 22.37$ ,  $df = 3$ ,  $p = 0.0001$ ; S,  $\chi^2 = 21.41$ ,  $df = 3$ ,  $p < 0.0001$ ). In experiment 1, larvae survived to the juvenile stage at 20–29°C and 25.5–34 ppt, with relatively higher survival rates at 23–26°C and 25.5–34 ppt

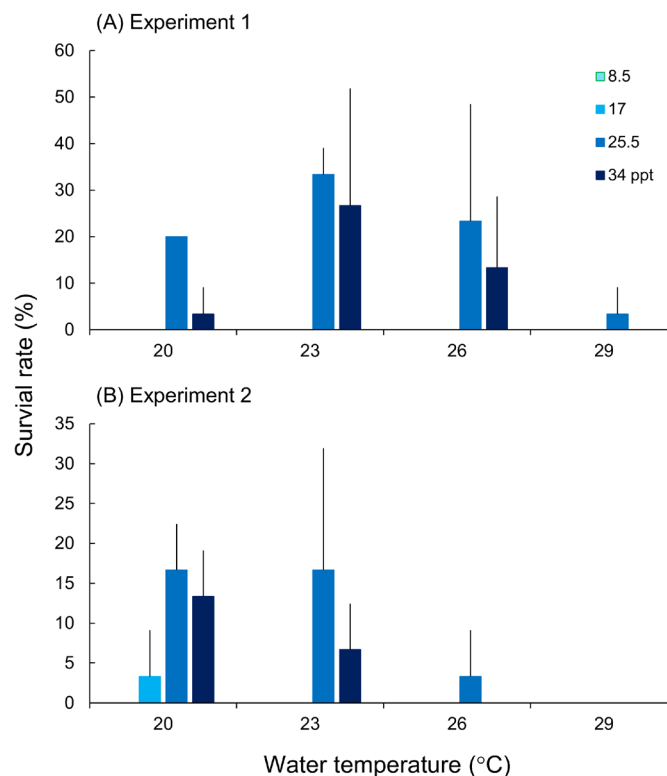


Fig. 1. Final larval survival rates to moult into the juvenile stage of *Caridina serratiostris* in experiments 1 (A) and 2 (B). Larvae were reared in three containers under the 16 combinations of four different temperatures (20, 23, 26 and 29°C) and salinity levels (8.5, 17, 25.5 and 34 ppt). Bars and vertical lines show mean and standard deviation values, respectively.

(Fig. 1A). At 8.5 ppt, all larvae died within ten days of hatching (Fig. S1). Although larvae did not reach the juvenile stage at 17 ppt, a small proportion of larvae survived for about two months (Fig. S1). In experiment 2, larvae survived to the juvenile stage at 20–26°C and 17–34 ppt, with relatively higher survival rates at 20–23°C and 25.5–34 ppt (Fig. 1B). All larvae died by 18 days after hatching under conditions of 8 ppt and 29°C, respectively (Fig. S2). In both experiments, larvae were frequently observed to be attracted to the surface tension of the rearing water in all culture conditions except for 8.5 ppt.

### Larval duration

Larval duration was significantly influenced by temperature but not by salinity in both experiments (experiment 1:  $n = 37$ ;  $T, \chi^2 = 81.85$ ,

$df = 3, p < 0.0001$ ;  $S, \chi^2 = 0.1502, df = 1, p = 0.6984$ ; experiment 2:  $n = 18$ ;  $T, \chi^2 = 34.17, df = 2, p < 0.0001$ ;  $S, \chi^2 = 1.026, df = 2, p = 0.5988$ ). The larval duration decreased with increasing temperature, lasting for about two months at 20°C and about one month at 26°C (Fig. 2).

### Larval growth

Temperature and salinity significantly affected the carapace length of the juveniles in experiment 1 ( $n = 36$ ;  $T, F = 12.89, df = 3, 10.9, p = 0.0007$ ;  $S, F = 17.92, df = 1, 6.2, p = 0.0052$ ) but not in experiment 2 ( $n = 17$ ;  $T, F = 3.383, df = 2, 6.4, p = 0.0995$ ;  $S, F = 2.527, df = 2, 7.8, p = 0.1424$ ). In both experiments, temperature and salinity tended to exhibit a negative effect on larval growth, but the carapace length of juveniles varied less between the test groups (Fig. 3).

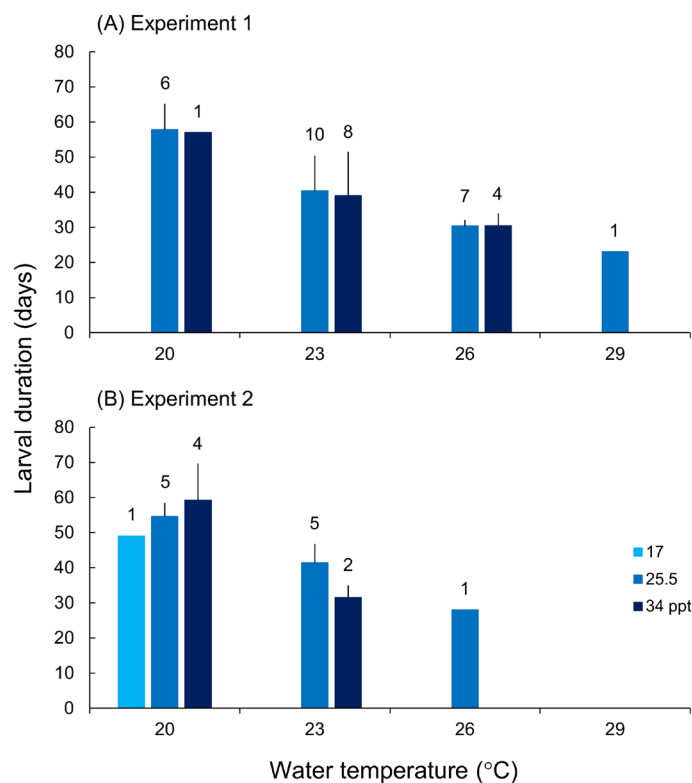


Fig. 2. Days required to moult into the juvenile stage (larval duration) of *Caridina serratiostris* in experiments 1 (A) and 2 (B). Larvae were reared under the 16 combinations of four different temperatures (20, 23, 26 and 29°C) and salinity levels (8.5, 17, 25.5 and 34 ppt). No larvae survived to the juvenile stage at 8.5 ppt. Bars and vertical lines indicate mean and standard deviation values, respectively. Numbers of individuals are shown above the bars.

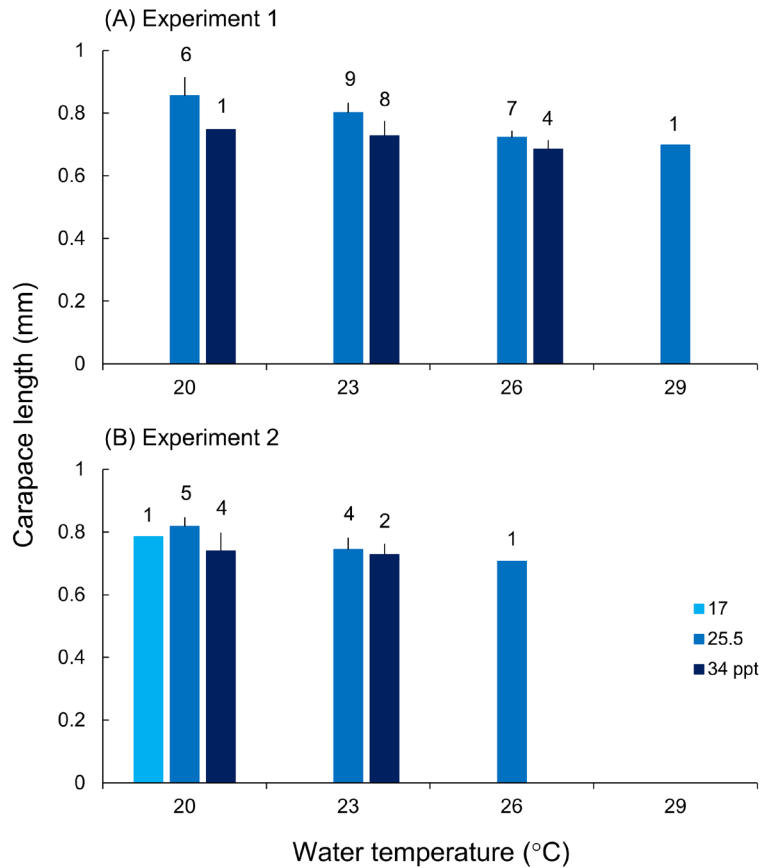


Fig. 3. Carapace length of juveniles of *Caridina serratiostris* in experiments 1 (A) and 2 (B). Larvae were reared under the 16 combinations of four different temperatures (20, 23, 26 and 29°C) and salinity levels (8.5, 17, 25.5 and 34 ppt) levels. No larvae survived to the juvenile stage at 8.5 ppt. Bars and vertical lines indicate mean and standard deviation values, respectively. Numbers of individuals are shown above the bars.

### Discussion

The present study demonstrated that temperature and salinity significantly affected the larval performance of *C. serratiostris* under laboratory conditions. Although the higher survival rates varied between the two experiments and were recorded at 23–26°C and 20–23°C in experiments 1 and 2, respectively (Fig. 1), larval survival responses to lower salinity and higher temperature conditions were similar between the experiments, with few or no larvae surviving to the juvenile stage at 8.5–17 ppt and 29°C (Fig. 1). Overall, appropriate temperature and salinity levels for the survival of *C. serratiostris* larvae were considered to be 20–26°C and 25.5–34 ppt.

We previously studied, under laboratory conditions, the dietary effects of phytoplankton and zooplankton on larval survival, duration and growth for four *Caridina* species: *C. leucosticta* Stimpson, 1860, *C. multidentata* Stimpson, 1860, *C. typus* H. Milne-Edwards, 1837, and *C. serratiostris* (Hamasaki et al. 2020a). The larvae were housed individually in the wells of six-well cell culture plates and were successfully cultured until metamorphosis into the juvenile stage in each species except for *C. serratiostris*, the larvae of which died due to being trapped in the water surface tension during the moulting process.

Previously, Nakahara et al. (2005) conducted a group culture of *C. serratiostris* larvae by

stocking 30 stage 1 zoeae in each of two 300 ml glass beakers containing 200 ml of rearing water (salinity: 0 and 25 ppt), without aeration, at 25–27°C, to which they supplied cultured *Tetraselmis tetrathele* at  $1 \times 10^5$  cells ml<sup>-1</sup>. They reported that larvae moulted to the juvenile stage at a mean survival rate of 53 % at 25 ppt, but that all larvae died within four days after hatching at 0 ppt. Consequently, in the present study, we adopted a group culture method using 100 ml beakers without aeration; however, larval attraction to the surface tension of the water was frequently observed, and the maximum survival rates of larvae to the juvenile stage were still low, at an average of 33 % (Fig. 1).

Hamasaki et al. (2020a) reported that the larvae of *C. leucosticta*, *C. multidentata* and *C. typus* were sometimes observed to be attracted to the water surface, but they could return to the water column in the culture wells. Larval attraction to the surface tension of the water may be a specific phenomenon in still water in small culture containers without aeration, but the reason why *C. serratirostris* larvae are vulnerable to the surface tension of water remains unknown. The effectiveness of larger rearing containers with their water surface ruffled by aeration should be tested to improve the survival of cultured larvae of *C. serratirostris*.

Larval culture experiments have been conducted for amphidromous atyid shrimps, including *C. leucosticta*, *C. multidentata*, *C. typus*, and *Paratya compressa* (De Haan, 1844), under 25 combinations of five different temperatures (20, 23, 26, 29 and 32°C) and five salinity levels (4.25, 8.5, 17, 25.5 and 34 ppt) (Hamasaki et al. 2021; Kondo et al. 2021). These larvae were stocked individually in the wells of six-well cell culture plates and fed *Tetraselmis* sp. at  $1 \times 10^5$  cells ml<sup>-1</sup> and rotifers at 20 individuals

ml<sup>-1</sup>. Kondo et al. (2021) reported the temperature and salinity range (and optimum range) for larval survival to the juvenile stage as: *C. leucosticta*, 20–29°C and 8.5–34 ppt (23–26°C and 17–25.5 ppt); *C. multidentata*, 20–32°C and 17–34 ppt (23–29°C and 17–25.5 ppt or 34 ppt); and *C. typus*, 20–29°C and 17–34 ppt (23–26°C and 17–25.5 ppt or 34 ppt). Hamasaki et al. (2021) documented that the survival rate of *P. compressa* larvae into the juvenile stage decreased linearly with increased temperature, and, although the larvae adapted to a wider range of salinity (8.5–34 ppt), larval mortality increased at high salinity (34 ppt) under higher temperature conditions. Among the atyid shrimp species, *C. serratirostris* larvae thus appear to adapt to a low-to-moderate temperature range (20–26°C) and to high salinity conditions (25.5–34 ppt).

It has been suggested that amphidromous shrimp species requiring lower salinities for larval development exhibit restricted larval dispersal, resulting in a genetically heterogenous population structure, and *vice versa* (Shokita 1979; Fujita et al. 2016; Kondo et al. 2021). In the northwest Pacific region, the western boundary current, i.e. the Kuroshio Current, plays an important role in transferring larvae of marine organisms from lower to higher latitudes through the Ryukyu Archipelago (24–30°N, 123–131°E) (Veron and Minchin 1992; Iida et al. 2010; Soeparno et al. 2012; He et al. 2015; Chang et al. 2018; Sanda et al. 2019). Considering the different larval survival responses to salinities, Kondo et al. (2021) inferred that the larval dispersal range may be most limited in *C. leucosticta*, moderate in the *C. typus*, whereas *C. multidentata* larvae may be able to disperse broadly under the high salinity conditions of the open sea. Hamasaki et al.



(2021) suggest that *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 barriers restricting larval dispersion northwards from the southern islands within the distributional area of this species. These marine larval dispersal patterns of the three *Caridina* species and *P. compressa* are supported by population genetic studies (Ikeda 1999; Fujita et al. 2016; Marin 2018).

Temperature significantly influenced the larval duration of *C. serratirostris*, but salinity affected it less (Fig. 2), as is generally true of decapod crustaceans (Anger 2001, 2003). The larval duration of *C. serratirostris* was extended from about one to two months at 20–26°C (Fig. 2). Sea surface areas with appropriate temperatures for the larval survival of *C. serratirostris* (~20–26°C) exist broadly around the Japanese coastal areas (Japan Meteorological Agency 2021) during the reproductive season [March to November off Okinawajima Island (26°45'N, 128°12'E) of the Ryukyu Archipelago (Shokita 1979); and June to October off the Boso Peninsula (34°58'N, 139°46'E) of mainland Japan (Hamasaki et al. unpublished data)]. However, sea areas with high temperatures (~30°C) can occur around the southern islands during summer. Therefore, *C. serratirostris* larvae may disperse broadly under the high salinity condition of the open sea (34 ppt), but high seawater temperatures during summer may restrict their northward ocean dispersal from the southern islands.

The carapace length of the *C. serratirostris* juveniles varied little under the different temperature and salinity conditions (Fig. 3). This is known to be true for *C. leucosticta*, *C. multidentata* and *C. typus* as revealed by Kondo

et al. (2021). They infer that *Caridina* juveniles did not exhibit the intraspecific variation in body size because juveniles may require a species-specific body size to ensure the physical status needed to accomplish migration to the adult habitat.

The present study revealed the larval performance of *C. serratirostris* under different temperature and salinity levels and inferred the larval dispersal pattern in the sea. However, the overall survival rate of larvae moulting into the juvenile stage was still low. To confirm the environmental adaptation and dispersal pattern of *C. serratirostris* larvae, further larval culture techniques with a higher survival rate into the juvenile stage will be required as well as a population genetic study.

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