

Occurrence of amphidromous atyid shrimps in a small stream on the Boso Peninsula, Japan

Ryota Yamada^{*1}, Keita Munakata^{*1}, Shigeki Dan, Katsuyuki Hamasaki^{*2}

Department of Marine Biosciences, Tokyo University of Marine Science and Technology, Konan, Minato, Tokyo 108-8477, Japan.

^{*1} These authors contributed equally to this article and share first authorship.

^{*2} Corresponding author, e-mail: hamak@kaiyodai.ac.jp

Abstract

The present study aimed to examine the relationship between stream temperature and the occurrence of amphidromous atyid shrimps as a basis for inferring the impacts of global warming on shrimp populations and communities. We investigated the occurrence of amphidromous atyid shrimps from spring 2017 to summer 2019 in the Banda River, a small stream located at near the southern tip of the Boso Peninsula, Japan. Five amphidromous atyids, including *Caridina leucosticta*, *C. multidentata*, *C. serratirostris*, *C. typus*, and *Paratya compressa*, were collected. The number of shrimps collected showed a distinct seasonal variation, being high in summer and low in winter. A positive correlation was found between the stream temperature and the number of shrimps collected. A notable reduction in shrimp occurrence was observed at temperatures below 15°C, particularly for *C. typus*, followed by *C. serratirostris*. Additionally, interspecific variability in shrimp occurrence was observed, likely due to interspecific differences in larval performance under changing ocean conditions. Global warming and climate change may affect the overwintering success and larval performance of atyids, potentially altering their population dynamics and community structure.

Key words: population dynamics, community structure, global warming, ocean climate change, larval dispersal strategy

Introduction

Freshwater shrimps of the family Atyidae (Decapoda: Caridea) are a very diverse group of decapod crustaceans. They are distributed worldwide, except in Antarctica, and are found in a variety of environments, from torrential mountain streams to slow oligohaline waters and rivers or streams within karst caves (De Grave et al. 2008; De Grave and Fransen 2011; Cai and Ng 2018). Atyid shrimps play an important role in the food webs and ecosystems of rivers and streams, acting 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 shrimp species exhibit one of two life history strategies: landlocked or amphidromous (Shokita 1979; Hayashi and Hamano 1984; Bauer 2013).

Landlocked species complete their entire life cycle in freshwater environments, whereas amphidromous species require saline water for larval development through to the juvenile stage (Shokita 1979; Hayashi and Hamano 1984; Nakahara et al. 2005; Hamasaki et al. 2021; Honda et al. 2021; Kondo et al. 2021). Adults of amphidromous shrimps live and reproduce in freshwater, but newly hatched larvae passively migrate to saline environments (Ideguchi et al. 2000, 2007; Hamano et al. 2005). Larval development proceeds in the brackish water of estuaries and coastal bays or in the open sea; then, juveniles migrate to adult freshwater habitats (Hamano and Hayashi 1992; Hamano et al. 2005; Bauer 2013; Yatsuya et al. 2013).

As ectotherms, the biological processes of atyid shrimps, such as behaviour, physiology, growth, and survival, should be strongly influenced by the thermal

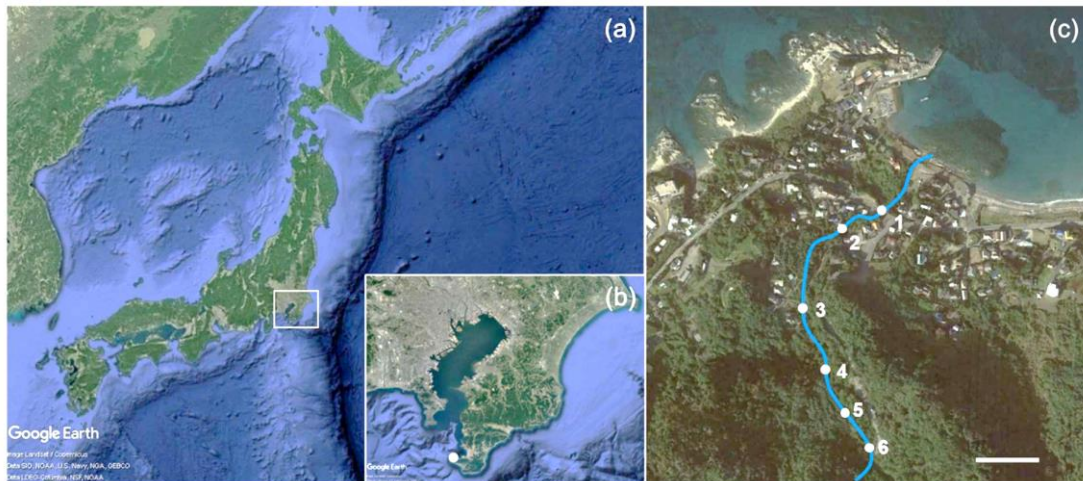


Fig. 1. Google Earth images showing the Japanese archipelago (a), the Boso Peninsula (b) and the survey sites where amphidromous atyid shrimps were collected in the Banda River (34°58'N, 139°46'E), a small stream on the Boso Peninsula, Japan (c). The white rectangle in panel (a) indicates the area including the Boso Peninsula. The white circle in panel (b) indicates the Banda River. The six survey sites 1–6 in the Banda River are shown in panel (c). The horizontal white line in panel (c) is a scale bar (100 m).

environment throughout their life cycle, as is known for various decapod crustaceans (Anger 2001; Green et al. 2014; Ren et al. 2021). Indeed, field studies conducted in rivers and streams have reported a notable reduction in the occurrence of the amphidromous atyid shrimps belonging to the genera *Caridina* and *Paratya* during the winter season in the temperate regions (34–35°N) of Japan (Hamano and Hayashi 1992; Imai and Oonuki 2022; Maruyama and Okamoto 2022). In contrast, there was a lesser decline observed in the subtropical regions (24–28°N) of Japan (Shokita 1979; Soomro et al. 2011). Furthermore, laboratory experiments have demonstrated interspecific variability in the ability of adult atyids to tolerate low temperatures (Maruyama and Okamoto 2022).

In the context of climate change, there has been an increase in air (terrestrial) and seawater (oceanic) temperatures (Houghton 2005; Hoegh-Guldberg and Bruno 2010; Japan Meteorological Agency 2023). This rise could potentially result in changes to the population dynamics and community structure of amphidromous atyid shrimps, as there may be an increase in overwintering success in a warming environment, depending on the low temperature

tolerance ability of each species. Thus, understanding the occurrence patterns of amphidromous atyid shrimps in relation to river and stream temperature is fundamental for inferring the impact of global warming on their future population dynamics and community structure. However, there is limited understanding of how temperature affects the occurrence of atyid shrimps in natural settings. The objective of this study was to investigate the relationship between water temperature and the presence of amphidromous atyid shrimps in the Banda River, a small stream located at near the southern tip of the Boso Peninsula (35°N), Japan. Our results highlight the temperature-dependent occurrence patterns of atyid shrimps in the Banda River. Additionally, we observed interspecific variability in the annual number of shrimps collected during our surveys for three consecutive years. We discuss the causes of this variability in terms of larval survival under ocean climate change.

Materials and Methods

Field study

We conducted this field study in the Banda River (34°58'N, 139°46'E), Boso Peninsula, Japan (Fig. 1a,

b). The Banda River is approximately 1.2 km long and supports five amphidromous atyids (Usami et al. 2008), namely *C. leucosticta* Stimpson 1860, *C. multidentata* Stimpson 1860, *C. serratirostris* De Man 1892, *C. typus* H. Milne-Edwards 1837, and *P. compressa* (De Haan 1844). These species have a wide distribution across western Japan, including the southern islands (i.e. Ryukyu Archipelago) (~24–35°N) (Shokita 1979; Hamano and Hayashi 1992; Suzuki et al. 1993; Usami et al. 2008; Watanabe and Kano 2009; Saito et al. 2012; Yatsuya et al. 2012; Soomro et al. 2016; Maruyama and Okamoto 2022).

Atyid shrimps exhibit species-specific longitudinal distributions in rivers and streams (Shokita 1979; Hamano and Hayashi 1992; Usami et al. 2008; Watanabe and Kano 2009; Saito et al. 2012; Yatsuya et al. 2012; Soomro et al. 2016). Therefore, to detect these five atyid shrimps, six survey sites (designated Sites 1 to 6) were established longitudinally between 150 m and 710 m from the river mouth at altitudes between 5 m and 15 m (Fig. 1c). Site 1, closest to the estuary, was a completely freshwater area unaffected by the tides. Each site covered an area of 4 m in length. We measured stream depth and width once at five points every 1 m along the centreline of each site to determine the relative differences in site profiles; the mean depth and width ranged between 23–71 cm and 56–326 cm, respectively (see [Table S1](#) and [Fig. S1](#) for profiles of each site). Site 1 was the widest and deepest, whereas Site 6 was the narrowest and shallowest. The substrates of Sites 1–4 and 6 were sand and/or pebbles with leaf litter, whereas Site 5 had a fast-flowing stream and many boulders.

Monthly surveys were conducted starting in May 2017, and the survey was planned to continue for full three years but was terminated in August 2019 due to the destruction of the survey sites by a typhoon in September 2019. The same two people visited each site once in the middle or late part of each month, and each person used a 28 cm scoop net to collect shrimps while moving pebbles and/or boulders on the surface

of the riverbed for 15 minutes in the afternoon. The mesh size of the scoop nets was changed from 5 mm to 2 mm in April 2018, with the aim of increasing the collection of newly recruited juveniles. Water temperature was measured at each survey site. In the present study, the four seasons are defined as: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).

Sample treatment

The collected shrimps were placed in an ice box and transported to a laboratory at the Tokyo University of Marine Science and Technology, Tokyo, Japan. They were then frozen in a –47 °C freezer. After thawing, the specimens from each survey site were identified and counted. Species identification was carried out according to Suzuki and Naruse (2011). The carapace length (CL) was measured to the nearest 0.01 mm for each specimen from the posterior margin of the orbit to the dorsal posterior end of the carapace using a stereomicroscope equipped with a digital camera and an image analysis system (Nikon Digital Sight and NIS-Elements software, Nikon Corp., Tokyo, Japan). The second pleopod was then removed from the specimen with forceps and examined under a microscope to determine sex based on the presence (male) or absence (female) of an appendix masculina on the endopod. Individuals smaller than the minimum size of males were considered to be juveniles. Females were recorded as ovigerous or non-ovigerous, and females larger than the smallest ovigerous female were considered to be mature females.

Statistical analysis

Statistical analyses were performed using R statistical software (R4.3.1; R Core Team 2023) at a 5 % significance level. The difference between the sexes in CL was evaluated using Welch's t-test. Spearman's rank correlation coefficient was

calculated to assess the similarity of spatial patterns of occurrence, that is, the total number of shrimps collected at each site during the survey period, between males and females or non-ovigerous and ovigerous females. Spearman's rank correlation coefficient was also used to infer similarity in temporal patterns of occurrence, that is, monthly number of shrimps collected, between males and females. As stream temperature did not vary between survey sites, temperature dependent occurrence of shrimps was assessed by analysing the relationship between mean stream temperature and the total number of shrimps collected at six survey sites in each month. This analysis was conducted using a Poisson generalised linear model (GLM). However, we detected model overdispersion (dispersion parameters > 1: i.e. 10.5 for *C. leucosticta*, 6.4 for *C. multidentata*, 18.0 for *C. serratiostris*, 25.1 for *C. typus*, and 24.2 for *P. compressa*) and thereby corrected the standard errors using a quasi-Poisson GLM (Zuur et al., 2009). The quasi-Poisson GLM analysis was performed using the *glm* function (log link).

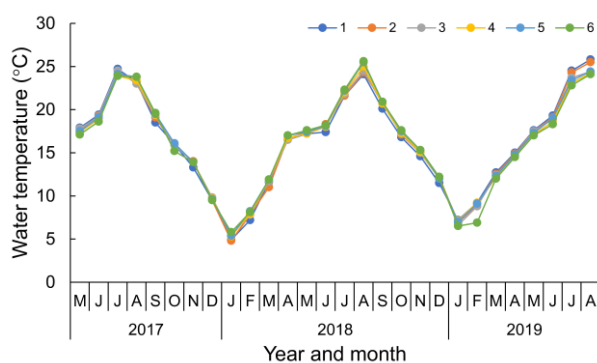


Fig. 2. Monthly water temperature records at survey sites 1–6 in the Banda River.

Results

Stream temperature and atyid shrimp collection

Monthly water temperature records at six survey sites are shown in Fig. 2. Water temperature did not vary between the survey sites but varied seasonally, with the highest records at 23–25 °C in summer (July

or August) and the lowest records at 5–7 °C in winter (January).

Table 1. Collection records of five amphidromous atyid shrimp species of the genera *Caridina* and *Paratyta* during field surveys conducted from May 2017 to August 2019 in the Banda River, Boso Peninsula, Japan.

Species	Number of shrimps			
	Juveniles	Males	Females (ovigerous)	Total
<i>C. leucosticta</i>	3	88	67 (8)	158
<i>C. multidentata</i>	4	333	147 (45)	484
<i>C. serratiostris</i>	0	275	454 (286)	729
<i>C. typus</i>	3	397	271 (95)	671
<i>P. compressa</i>	24	3574	2053 (407)	5651

Five amphidromous atyid shrimp species were collected, and the total number of individuals collected during the study period was highest for *P. compressa* (5651), followed by *C. serratiostris* (729), *C. typus* (671), and *C. multidentata* (484), with the lowest number recorded for *C. leucosticta* (158) (Table 1). The following monthly collection records are summarised for each species (Tables S2–S6): number of juveniles, males, females, mature females and ovigerous females and proportion of ovigerous females to mature females with information on minimum size of males and ovigerous females.

The number of juveniles collected during the survey period was low in each species, ranging from 0 to 24 (Table 1), despite reducing the mesh size of the scoop nets from April 2018. Ovigerous females were observed in all species (Table 1), indicating that both sexes can mature and breed within the Banda River. The body size (CL) was significantly larger in females than in males (Fig. 3; see Table S7 for means and standard deviations of CL and corresponding test statistics).

Figure 4 shows the number of juveniles, males, non-ovigerous females, and ovigerous females collected at each survey site for each species. The spatial occurrence pattern was similar between males and females or between ovigerous and non-ovigerous females, as the Spearman's rank correlation co-

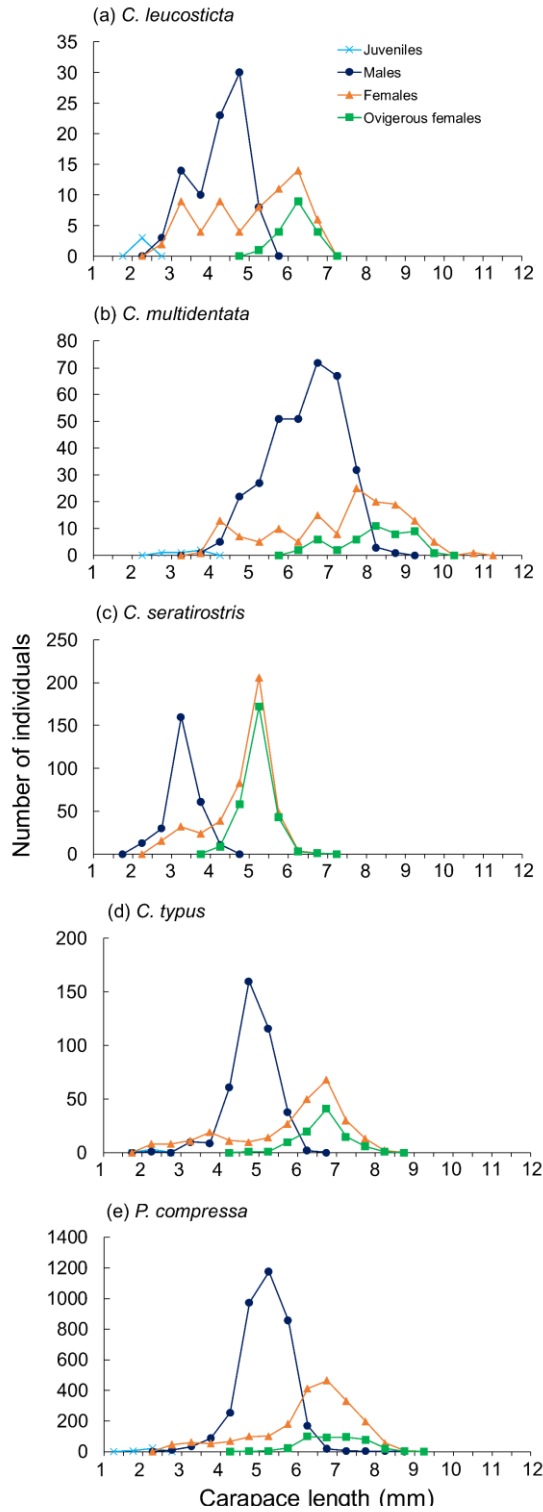


Fig. 3. Carapace length frequency distributions of juveniles, males, females, and ovigerous females collected during the survey period in the Banda River for five amphidromous atyid shrimp species of the genera *Caridina* and *Paratya*: *C. leucosticta* (a), *C. multidentata* (b), *C. serratiostris* (c), *C. typus* (d), and *P. compressa* (e).

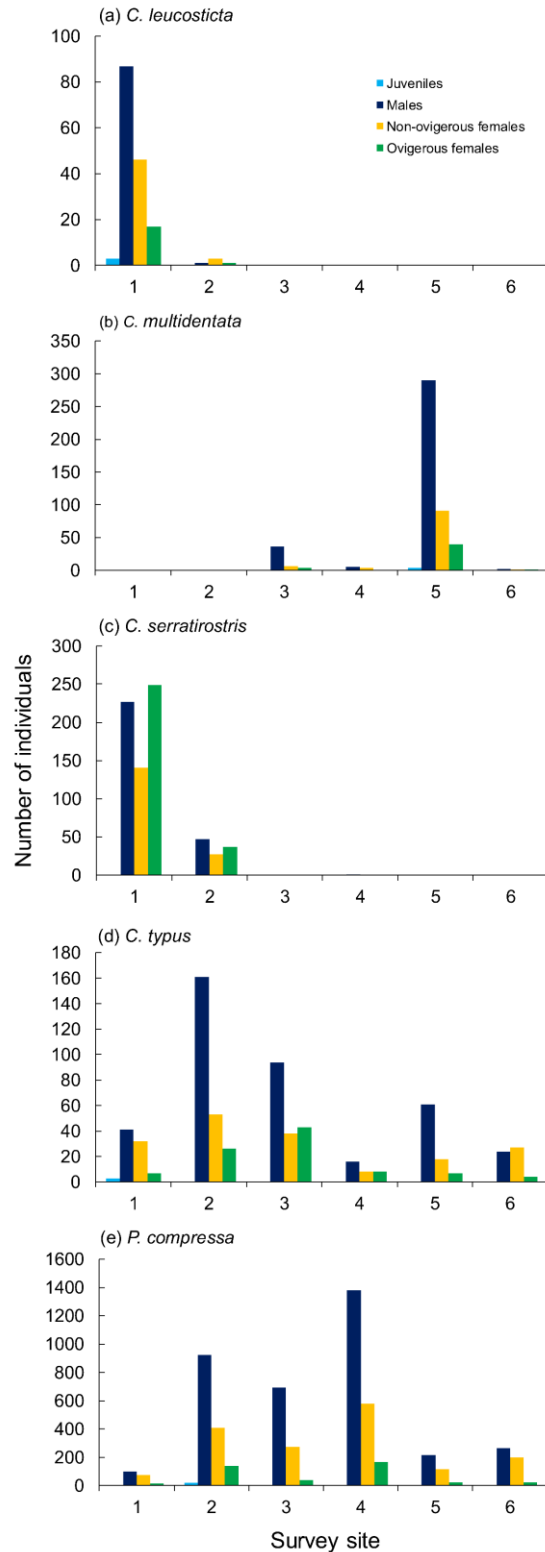


Fig. 4. Number of juveniles, males, non-ovigerous females, and ovigerous females collected at each survey site during the survey period in the Banda River for five amphidromous atyid shrimp species of the genera *Caridina* and *Paratya*: *C. leucosticta* (a), *C. multidentata* (b), *C. serratiostris* (c), *C. typus* (d), and *P. compressa* (e).

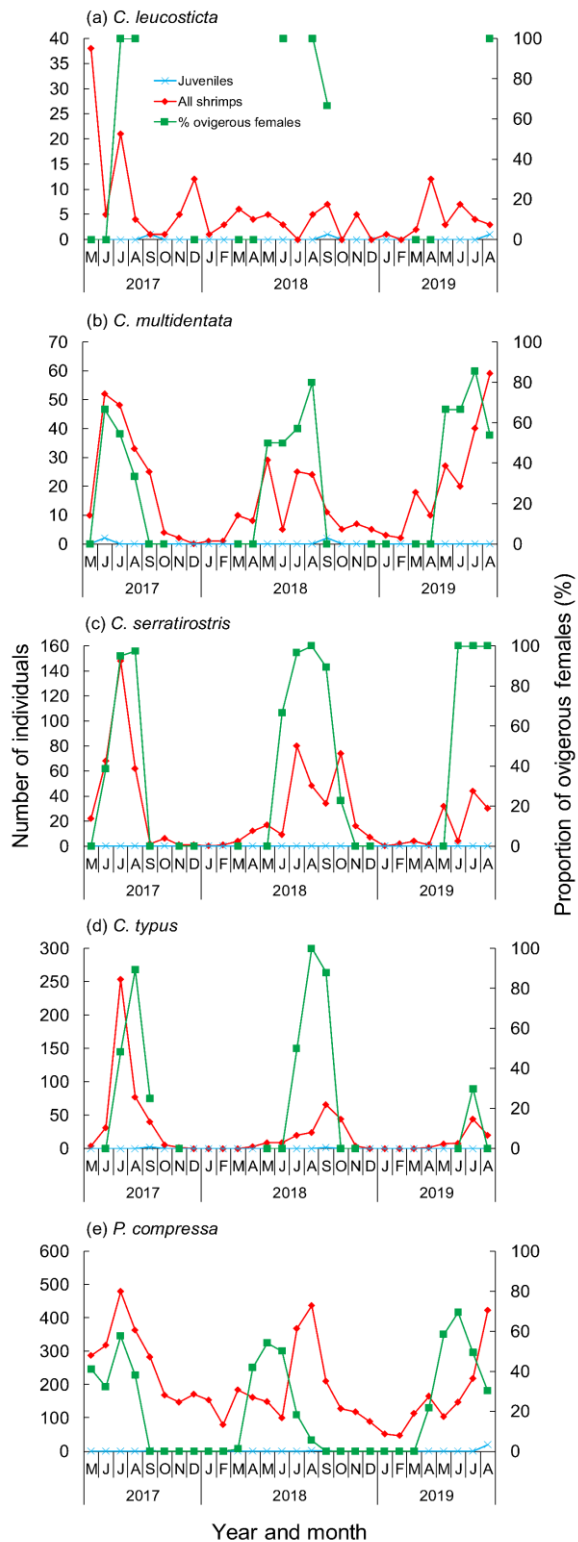


Fig. 5. Number of juveniles and all shrimps collected in each month during the survey period and the proportion of ovigerous females to mature females in each month in the Banda River for five amphidromous atyid shrimp species of the genera *Caridina* and *Paratya*: *C. leucosticta* (a), *C. multidentata* (b), *C. serratiostris* (c), *C. typus* (d), and *P. compressa* (e). The proportion of ovigerous females was not calculated when mature females were not collected.

efficient between the number of shrimps collected at survey sites was statistically significant for all species (males and females: $\rho = 0.898-1$, $P = 0.0028-0.0151$ or < 0.0001 ; ovigerous and non-ovigerous females: $\rho = 0.832-1$, $P = 0.0167-0.0401$ or < 0.0001), except for *C. typus* (males and females: $\rho = 0.771$; $P = 0.1028$; ovigerous and non-ovigerous females: $\rho = 0.493$; $P = 0.3206$) (Table S8). *Caridina leucosticta* and *C. serratiostris* were mainly found at Site 1 and *C. multidentata* was mainly found at Site 5. Although the correlation between the occurrence of males and females or between ovigerous and non-ovigerous females was not statistically significant for *C. typus*, they were found in all the survey sites, being abundant in Sites 2 and 3. *Paratya compressa* was also found in all the survey sites, particularly Sites 2, 3, and 4.

Atyid shrimp occurrence

The temporal pattern of occurrence, that is, the monthly number of shrimps collected, was highly correlated between males and females (Tables S2–S6), as the significantly high Spearman's rank correlation coefficients between these variables were observed for all species ($\rho = 0.794-0.870$; $P < 0.0001$), except for *C. leucosticta* with a relatively low coefficient ($\rho = 0.422$; $P = 0.0254$) (Table S9).

Figure 5 shows the number of juveniles and all shrimps collected and the proportion of ovigerous females to mature females in each month for each species. The number of shrimps collected in three consecutive years did not vary much for *C. multidentata* and *P. compressa*, and it decreased for *C. leucosticta*, *C. serratiostris*, and *C. typus* (Fig. 5). Nevertheless, atyid shrimps, with the exception of *C. leucosticta*, showed a distinct seasonal pattern of occurrence, with the number of shrimps collected being high from late spring (May) through summer (June to August) to early (September) or mid-autumn (October) and low in winter (December to February). The quasi-Poisson GLM analysis identified a

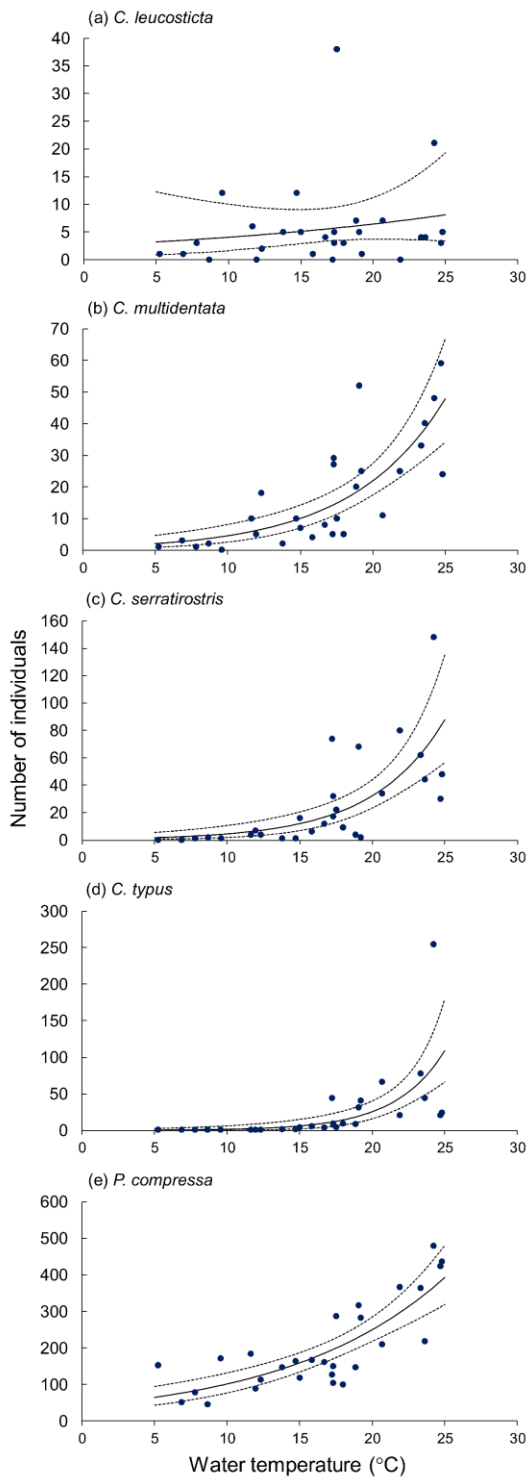


Fig. 6. The relationship between monthly mean water temperature at the survey sites and the number of shrimps collected in each month during the survey period in the Banda River for five amphidromous atyid shrimp species of the genera *Caridina* and *Paratya*: *C. leucosticta* (a), *C. multidentata* (b), *C. serratiostris* (c), *C. typus* (d), and *P. compressa* (e). Fitted lines are drawn based on the coefficient estimates of the quasi-Poisson generalised models shown in Table 2. The dotted lines indicate the 95 % confidence intervals.

Table 2. Coefficient estimates with standard errors (SE) of quasi-Poisson generalised linear models to evaluate the relationship between monthly collected numbers of five amphidromous atyid shrimp species of the genera *Caridina* and *Paratya* (response variable) and mean water temperature at six survey sites during 28 field surveys from May 2017 to August 2019 (explanatory variable) in the Banda River, Boso Peninsula, Japan.

Species	Coefficient	Estimate	SE	t value	p
<i>C. leucosticta</i>	Intercept	0.9553	0.9074	1.053	0.3020
	WT	0.0455	0.0492	0.925	0.3640
<i>C. multidentata</i>	Intercept	-0.0296	0.5471	-0.054	0.9570
	WT	0.1559	0.0264	5.907	< 0.0001
<i>C. serratiostris</i>	Intercept	-0.5476	0.8486	-0.645	0.5240
	WT	0.2008	0.0396	5.067	< 0.0001
<i>C. typus</i>	Intercept	-2.5947	1.3471	-1.926	0.0651
	WT	0.2914	0.0600	4.856	< 0.0001
<i>P. compressa</i>	Intercept	3.7082	0.2595	14.290	< 0.0001
	WT	0.0906	0.0133	6.800	< 0.0001

significant positive relationship between water temperature and the number of shrimps collected for all species, except for *C. leucosticta* (Fig. 6; Table 2). No *C. typus* and few *C. serratiostris* were collected from late autumn (November) to early/mid spring (March/April) when stream temperature was below 15 °C, and the number of *C. leucosticta* and *C. multidentata* tended to be higher than *C. serratiostris* and *C. typus* during these periods (Figs. 5 and 6; Tables S2–S6). In addition, the number of *P. compressa* was much higher than *Caridina* species in winter. Based on the occurrence of each species in winter, the coefficient of estimate of the quasi-Poisson GLM was highest for *C. typus* (0.2914), followed by *C. serratiostris* (0.2008) and *C. multidentata* (0.1559), with the lowest observed in *P. compressa* (0.0906) (Table 2).

Ovigerous females occurred during the warm seasons from spring to autumn: *C. leucosticta*, June to September (18.0–24.8 °C); *C. multidentata*, May to August (17.3–24.8 °C); *C. serratiostris*, June to October (17.2–24.8 °C); *C. typus*, July to September (19.2–24.8 °C); and *P. compressa*, April (rarely March) to August (14.7–24.8 °C) (Fig. 5).

Atyid shrimp growth and maturity

The growth pattern of new recruits could be

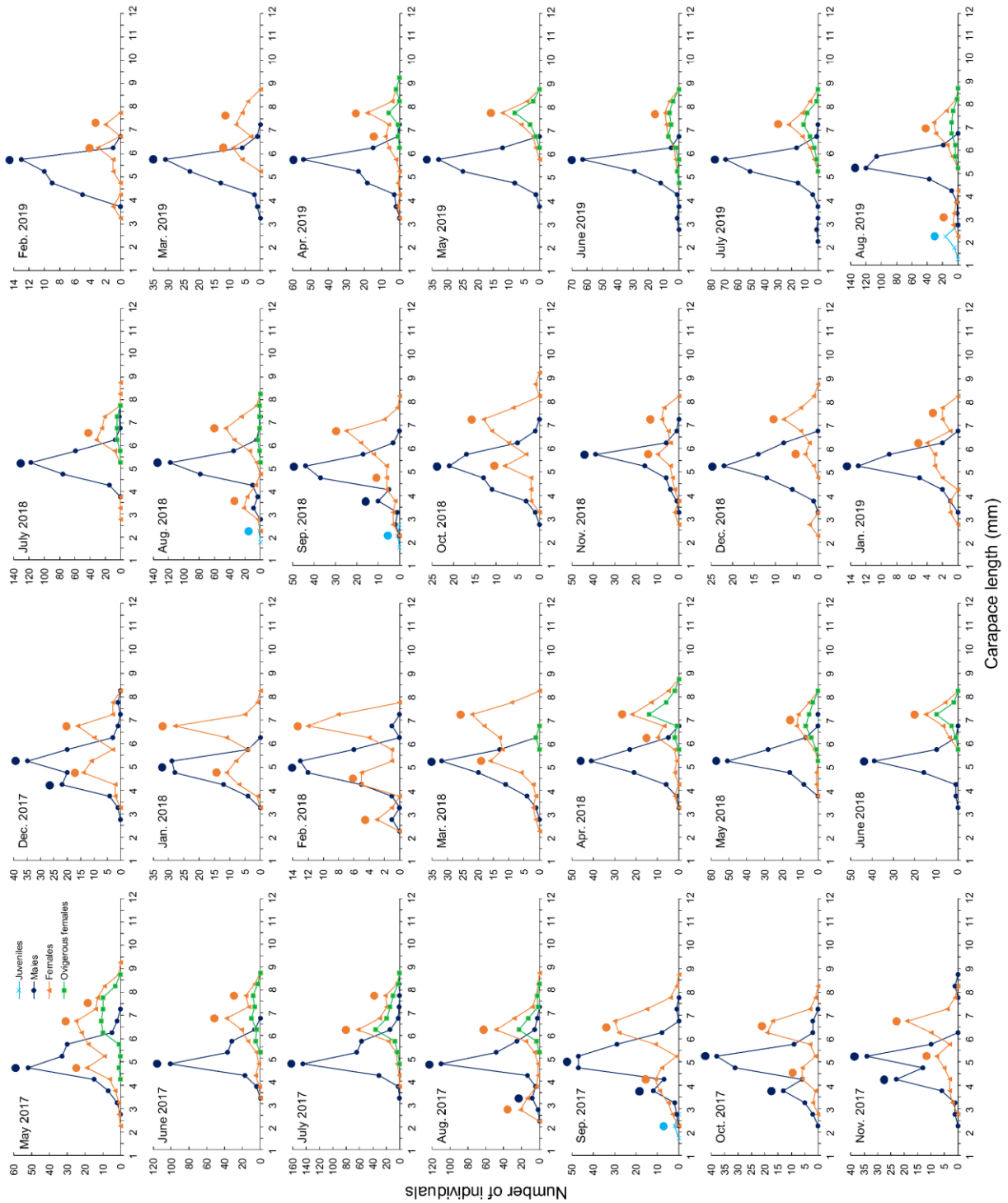


Fig. 7. Carapace length frequency distributions of *Paratya compressa* juveniles, males, females and oviparous females collected from the Banda River between May 2017 and August 2019. Light blue circles indicate the juveniles, and dark blue and orange circles indicate the distinct modal values of males and females, respectively.

followed only for *P. compressa* with the highest collected number among the target species (Fig. 7). According to the modal values in the size frequency distributions, recruitment started in August and new recruits with 2–3 mm CL tended to grow linearly until the end of autumn (November) in both sexes, reaching a similar body size as adult males. Females resumed growth in spring (March), reaching a body size similar to adult females in late spring (April and May) and starting to produce eggs. Thus, *P. compressa* females reproduced at one year of age.

Discussion

Atyid shrimp collection

Five amphidromous atyid shrimp species were collected from the Banda River during our field surveys conducted from May 2017 to August 2019, with *P. compressa* being the most abundant, followed by *C. serratiostris*, *C. typus*, and *C. multidentata*, and the least abundant species was *C. leucosticta* (Table 1). Our results are consistent with those of Usami et al. (2008), who collected atyid shrimps once in the Banda River in the summer of 2007, although *C. serratiostris* was less abundant in their survey than in the present study.

Atyid shrimps are known to exhibit species-specific longitudinal distributions generated by the topographic profiles of rivers and streams, their migratory capacity and microhabitat preferences (Shokita, 1979; Usami et al. 2008; Saito et al. 2012; Yatsuya et al. 2012). In the Banda River, distribution patterns of atyid shrimps similar to those typical of small streams and rivers in temperate regions of Japan (Usami et al. 2008; Saito et al. 2012) were observed as follows: (1) *C. leucosticta* and *C. serratiostris* inhabited the lower reaches, particularly Site 1; (2) *C. multidentata* occurred mainly in the upper reaches (Site 5) with a fast flow on boulders; and (3) *C. typus* and *P. compressa* were found in all survey sites and were abundant in the lower-middle reaches with leaf litter on sand and/or pebbles (Sites 2 and 3 for *C.*

typus and Sites 2–4 for *P. compressa*) (Fig. 4). These longitudinal distribution patterns of amphidromous atyid shrimps in the Banda River were also observed in the survey conducted by Usami et al. (2008).

In our surveys, *C. leucosticta* was the least abundant. Ideguchi and Yamahira (2004) investigated the relationship between the abundance of *C. leucosticta* and *C. typus* and environmental characteristics, such as flow rate and artificial structures, in 75 rivers in Fukuoka Prefecture, western Japan. They found a difference in occurrence pattern of *C. leucosticta* and *C. typus* in relation with flow rate; e.g. *C. leucosticta* was more abundant in rivers with higher flow rates, while *C. typus* was found only in rivers with lower flow rates. *Caridina leucosticta* is abundant in the lower reaches of small and medium-sized rivers and streams with > 7 km long (Yamahira et al. 2007; Usami et al. 2008; Watanabe and Kano 2009; Saito et al. 2012; Yatsuya et al. 2012, 2013). *Caridina leucosticta* could potentially have the lowest abundance in the Banda River's restricted lower reaches with smaller flows.

Temperature dependent occurrence of atyid shrimps

In this study, shrimp occurrence varied seasonally with stream water temperature for all species except *C. leucosticta*, which was the least abundant (Figs. 2 and 5). The number of shrimps collected was generally high in summer and low in winter, as previously observed for the same atyid shrimp species in temperate regions of Japan (Hamano and Hayashi 1992; Imai and Oonuki 2022; Maruyama and Okamoto 2022). However, the present study clearly detected the positive relationship between stream temperature and the number of shrimps collected for atyids and showed that the number of shrimps collected decreased greatly at temperatures below 15 °C (Fig. 6). The biological processes of ectothermic atyid shrimps are strongly influenced by the thermal environment. For example, Maruyama

and Okamoto (2022) investigated the low temperature tolerance of adults of five atyid shrimp species by reducing the culture temperature from 10–13 °C to 1 °C at a rate of 1 °C/day. The authors reported the following: *P. compressa*, all survived at 1 °C; *C. multidentata*, all survived at 5 °C and 36 % survived at 1 °C; *C. leucosticta*, all survived at 10 °C and 17 % survived at 1 °C; *C. serratirostris*, all survived at 4 °C and all died at 2 °C; and *C. typus*, all survived at 11 °C and all died at 7 °C. Thus, there is interspecific variability in the ability of atyids to tolerate low temperatures. The ability to tolerate low temperatures seems to be strongest in *P. compressa*, followed by *C. multidentata*, *C. leucosticta*, and *C. serratirostris*, with *C. typus* reporting the weakest tolerance.

Differences in low-temperature adaptation among atyids may account for the interspecific variability in the number of shrimps collected during winter in the Banda River, which was greatest for *P. compressa*, followed by *C. leucosticta*, *C. multidentata*, and *C. serratirostris*, and lowest for *C. typus* (Fig. 6). The temperature of the Banda River dropped to 5–7 °C in winter (January) (Fig. 2), which is below the lethal temperature (7–11 °C) for *C. typus* reported by Maruyama and Okamoto (2022). Therefore, some *C. typus* may die in winter in the Banda River, but some may overwinter in habitats where the temperature is maintained above the lethal temperature, as *C. typus* adults were collected in spring, as observed for other atyid shrimps (Figs. 3 and S2). Taken together, atyid shrimps may become inactive below 15 °C and overwinter in habitats above lethal temperatures under gravel and rocks or in deeper pools where scoop net sampling was not possible, as previously suggested by Imai and Oonuki (2022) and Maruyama and Okamoto (2022). Identifying and protecting overwintering microhabitats is crucial for the conservation of atyid shrimps (Maruyama and Okamoto 2022). Additionally, sampling methods should be developed to collect shrimps in winter to

assess the survival of atyids during the overwintering period.

Less seasonal variation in atyid occurrence has been observed in rivers and streams in subtropical regions where winter temperatures are above 15 °C, and reproductive seasons tend to start earlier (Shokita 1979; Soomro et al. 2011) than in temperate regions (Hamano and Hayashi 1992; Yamahira et al. 2007; Imai and Oonuki 2022; the present study). Similar phenomena have also been observed for *C. typus* in a river in a temperate region where general winter temperatures were above 15 °C due to the inflow of hot spring water (Maruyama and Okamoto 2022). High-temperature regimes can accelerate the physiological process of ectotherms; thus, the longevity of *Caridina* species seems to be shorter in subtropical populations (1.5 years) (Shokita 1979) than in temperate populations (2–3 years) (Hamano and Hayashi 1992; Yamahira et al. 2007; Imai and Oonuki 2022). Global warming may alter the population dynamics and community structure of atyids by affecting overwintering success and accelerating reproduction and life cycles in temperate populations.

Whilst the atyid shrimps' low temperature tolerance has been considered in this study, the high temperature tolerance requires clarification for a comprehensive assessment of the impact of global warming on atyid shrimp populations and communities.

Annual abundance of atyid shrimps

The annual number of shrimps collected showed interspecific variability: it did not vary much for *C. multidentata* and *P. compressa* and decreased for *C. leucosticta*, *C. serratirostris* and *C. typus* (Fig. 5). Amphidromous atyid shrimps consist of metapopulations linked by marine larval dispersal (Fujita et al. 2016). Therefore, their larval survival and development in the sea should influence the recruitment of juveniles to freshwater environments.

The western boundary current, the Kuroshio (Fig. S3a, b), is known to strongly influence marine resources by altering current circulation and abiotic and biotic environments, such as temperature, salinity, nutrients, and plankton (Ogawa and Wakabayashi 1992; Nakata et al. 2000). The Boso Peninsula is the northernmost region where marine biodiversity is directly influenced by the Kuroshio in the northwestern Pacific (Hagiwara 2003; Yamano and Namizaki 2009; Yamano et al. 2011; Sunobe et al. 2014; Sanda et al. 2019; Inutsuka et al. 2020; Itsukushima and Kano 2021).

Our field study commenced in spring 2017, and the Kuroshio has taken the large meander (LM) path since summer 2017 (Fig. S3c, d). Ocean climate changes are known to occur during the LM path periods: the westward Kuroshio bifurcation occurs around 138°E, 34°N and transports the warm water (+1–2 °C) into the coastal region (Sugimoto et al. 2020). The longevity of atyid shrimps in temperate regions of Japan is considered to be more than one year (Hamano and Hayashi 1992; Yamahira et al. 2007; Imai and Oonuki 2022; the present study). Therefore, atyid shrimps aged 1+ collected in 2018 and 2019 in our surveys are considered to have spent their marine larval life when the Kuroshio showed the LM path. Laboratory experiments have shown that larvae of *C. leucosticta*, *C. multidentata*, *C. serratiostris*, *C. typus* and *P. compressa* survive and develop into juveniles over a wide range of temperatures (20–29 °C) (Hamasaki et al. 2021; Honda et al. 2021; Kondo et al. 2021). Sea areas above 29 °C are not observed along the Pacific coast of mainland Japan during the high reproductive season of atyids in summer (Fig. S4). Therefore, environmental factors other than seawater temperature may affect the survival of atyid larvae in the sea.

Negative chlorophyll *a* anomalies are observed during the LM path periods—that is, phytoplankton decline in the nearshore regions of the central Pacific coast (Lizarbe Barreto et al. 2021). Laboratory

experiments have documented that atyid shrimp larvae survive and develop into juveniles by feeding on phytoplankton: *P. compressa* larvae were able to develop to the juvenile stage under poor feeding conditions that did not support larval development of *Caridina* larvae (Hamasaki et al. 2020a, 2020b), and *C. multidentata* larvae were able to extend larval duration under limited feeding conditions compared to other *Caridina* species (Hamasaki et al. 2020a). Survival to the juvenile stage may have been maintained for *P. compressa* larvae adapted to oligotrophic conditions, and the likelihood of colonising the rivers and streams may have been maintained for *C. multidentata* larvae, which have the ability to tolerate oligotrophic conditions and extend the duration of development to the juvenile stage.

Conclusions

Our field surveys quantified the temperature-dependent occurrence patterns of five amphidromous atyid shrimps—*Caridina leucosticta*, *C. multidentata*, *C. serratiostris*, *C. typus*, and *Paratya compressa*—in the Banda River, a small stream on the Boso Peninsula, temperate Japan. Global warming may alter the population dynamics and community structure of atyids by affecting their overwintering success, depending on species-specific adaptation to low temperatures. Atyid shrimps may overwinter in habitats above lethal temperatures. Identifying and protecting overwintering microhabitats is essential for the conservation of atyid shrimps. Atyid shrimp populations and communities appear to be influenced by the path of the Kuroshio, which affects larval survival in the sea. Monitoring the occurrence of amphidromous atyids in the temperate regions can inform us of the extent of global warming under ocean climate change.

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