Occurrence and distribution of freshwater shrimp in the Isazu and Yura Rivers, Kyoto, western Japan

MIWA YATSUYA1,*, MASAHIRO UENO2 & YOH YAMASHITA3

1 Seikai National Fisheries Research Institute, Fisheries Research Agency, 1551–8 Taira-machi, Nagasaki 851–2213, Japan
2 Maizuru Fisheries Research Station, Field Science Education and Research Center, Kyoto University, Nagahama, Maizuru 625–0086, Japan
3 Field Science Education and Research Center, Kyoto University, Kitashirakawa Oiwake-cho, Kyoto 606–8502, Japan

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Abstract: Seasonal occurrence and longitudinal distribution patterns of freshwater shrimp were investigated in two rivers in western Japan. Four species of the family Atyidae and two species of Palaemonidae were observed. Water temperature and life cycle patterns of these shrimps affected their seasonal occurrence. The amphidromous shrimp species *Caridina leucosticta*, *Caridina serratiostris*, and *Macrobrachium nipponense* were distributed within a brackish estuary and the lower reaches of rivers, while the landlocked shrimp species *Paratya improvisa*, *Neocaridina denticulata*, and *Palaemon paucidens* were found in the lower and middle reaches. The biomass of all shrimp in each sampling area measured between December and March ranged from 0.49 to 34.72 g m⁻¹ (wet weight in grams per meter of river bank) in the Isazu River with relatively dense riverbank vegetation, and from 0.06 to 1.22 g m⁻¹ in the Yura River with less riparian vegetation. Environmental factors such as stream gradient, distance to saltwater intrusion, structure of riverbank habitat, and the life history of each species were important factors in determining their longitudinal distribution.

Key words: freshwater shrimp, life history, longitudinal distribution, river habitat, seasonal variation

Introduction

Japan has 42 species of freshwater shrimp (Decapoda: Caridea): 24 species in the family Atyidae, 17 in the Palaemonidae, and 1 in the Alpheidae. There are 9 atyid species extant in temperate areas of Japan and 10 palaemonids (Hayashi 2011). Some freshwater shrimp are amphidromous and others are landlocked (see reviews by Bauer & Dalahoussaye 2008, Bauer 2011).

Freshwater shrimp are important components of stream food webs, with atyids being primary consumers and palaemonids primary or secondary consumers (Covich & McDowell 1996). Herbivorous and detritivorous atyid species influence algal production, leaf litter breakdown, and benthic community structure (Pringle et al. 1993, Covich et al. 1999, Crowl et al. 2001). Despite their ecological importance, freshwater shrimp are threatened by anthropogenic modifications. Dams and water gates interrupt the upstream migration of amphidromous shrimp (Miya & Hamano 1988, Holmquist et al. 1998). Riverbank modifications such as channelization and the removal of streamside vegetation can reduce and fragment the shrimp habitat (e.g. Martin et al. 2009). In Japan, several freshwater shrimp species are listed as endangered, vulnerable, or near threatened species by the Ministry of the Environment and prefectural governments (reviewed by Saito 2011).

For the effective conservation of freshwater shrimp populations and their habitats, it is necessary to obtain detailed information on their distribution and understand the factors determining the distribution of each species. There are some previous reports regarding the geographical and longitudinal distribution of freshwater shrimp in Japan (Shokita 1975, 1979, Miya & Hamano 1988, Suzuki et al. 1993, Niwa & Yokoyama 1993, Usami et al. 2008). Several studies have documented that the longitudinal distribution of amphidromous shrimps is generally affected by riverbed gradients, locations of physical obstacles for upstream migration (natural cascades and artificial dams), and the
climbing ability of shrimp (Shokita 1975, 1979, Miya & Hamano 1988, Suzuki et al. 1993). However, details of the factors determining the distribution of landlocked shrimps are incompletely understood. In addition, relatively little information is available on shrimp distribution in rivers along the coastline of the Sea of Japan (see, for example, Kamita 1970, Hamano et al. 2005) compared to the Pacific coastline. The present study compares and analyzes the seasonal occurrence and longitudinal distribution of freshwater shrimp in two rivers that flow into the western part of Wakasa Bay, Sea of Japan. The aim was to document shrimp occurrence and distribution related to river morphology and habitat conditions.

**Materials and methods**

**Study sites**

The Isazu River (17.9 km long, drainage area 75 km²) and the Yura River (146 km long, drainage area 1,880 km²) are located in northern Kyoto Prefecture (35°N, 135°E), Japan. The Isazu River flows into Maizuru Bay and the Yura River flow into the Tango Sea in the western part of Wakasa Bay (Fig. 1). River discharge typically increases from February to April due to snow melt-water, and shows a sudden increase from July to October due to rainfall associated with low pressure systems or typhoons (Kasai et al. 2010). Seawater intrudes up to 1.1 km upstream in the Isazu River (Yatsuya et al., personal observation) and up to 18 km upstream in the main stream of the Yura River, mostly from August to December depending on river discharge and sea level (Kasai et al. 2010). The effect of the diel tidal fluctuation (less than 0.5 m in both rivers) on the physical condition of the estuary is negligible (Kasai et al. 2010).

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**Sampling stations**

Monthly sampling from October 2005 to November 2006 was conducted at two stations in the Isazu River (Fig. 1) 1.6 km (denominated to be Stn. 1.6) and 2.0 km (Stn. 2.0) from the river mouth (Table 1). However, sampling was not possible in January and February 2006 because of heavy snow and high water levels. Shrimps were also collected at 10 locations from the lowest station (Stn. 1.1) to

| Distance from the river mouth (km) | Main stream (M) or Tributaries (T) | Sampling month | # of sampling | Reach section | Reach type * | Stream order ** |
|-----------------------------------|-------------------------------------|----------------|---------------|---------------|--------------|----------------|
| 1.1                               | M                                   | Aug. 2006, Sep. 2006 | 2             | Estuary       | Bc           | 4              |
| 1.0                               | M                                   | Oct. 2005–Nov. 2006 | 10            | Lower         | Bc           | 4              |
| 2.0                               | M                                   | Oct. 2005–Nov. 2006 | 10            | Lower         | Bb–Bc        | 4              |
| 2.5                               | M                                   | Jul. 2006         | 1             | Lower         | Bb–Bc        | 4              |
| 2.9                               | M                                   | Oct. 2005, Dec. 2005 | 2             | Lower         | Bb–Bc        | 4              |
| 4.0                               | M                                   | Dec. 2005         | 1             | Lower         | Bb–Bc        | 4              |
| 4.7                               | M                                   | Oct. 2005, Dec. 2005 | 2             | Lower         | Bb           | 3              |
| 6.4                               | M                                   | Mar. 2006         | 1             | Middle        | Bb           | 3              |
| 8.1                               | M                                   | Mar. 2006         | 1             | Middle        | Bb           | 3              |
| 12.2                              | M                                   | Mar. 2006         | 1             | Middle        | Bb           | 3              |
| 14.5                              | M                                   | Mar. 2006         | 1             | Middle        | Bb           | 3              |
| 16.9                              | M                                   | Jun. 2005         | 1             | Upper         | Aa           | 1              |

* Based on the Kani’s classification (Kani 1978, Tamada 2011).
** Based on Strahler (1957).
the upper stream (Stn. 16.9) once or twice from June 2005 to September 2006 (Fig. 1, Table 1).

In the Yura River, the lower reach and brackish estuary (4.4–49.4 km from the river mouth) were surveyed (Fig. 1, Table 2). Sampling was conducted at five stations along the main stream and six stations along tributaries (from May to June 2007), and at 18 stations along tributaries (from December 2008 to January 2009) (Table 2). At tributary stations, sampling was conducted near the tributary’s junction with the main stream (up to 200 m from the junction).

To analyze shrimp distribution in relation to river morphology, sampling stations were divided according to reach sections, reach types, and stream orders. The classification of reach sections followed the above-mentioned four classes: upper, middle, and lower reaches and the brackish estuary. All stations along tributaries of the Yura River were classified into lower stations even if the junction with the main stream was located in the brackish estuary, because seawater rarely intruded into the tributaries due to the large inclination observed at the junction. Therefore, the lowest station (1.1) in the Isazu River and 4 stations (12.8, 14.6, 16.6, 17.8) in the Yura River were classified as brackish estuary; 6 stations (1.6–4.7) in the Isazu River and 19 stations (4.4–11.1, 13.8, 14.8, 15.3, 18.4–49.4) in the Yura River including all tributary stations were classified as lower reach; 4 stations (6.4–14.5) in the Isazu River were considered middle reach; and the uppermost station (16.9) of the Isazu River was the sole upper stream station (Tables 1, 2).

Classification of reach type followed Kani (1978) and Tamada (2011). Type A is defined as a stream segment with more than one riffle/pool sequence between meander bends, and type B is defined as having only one riffle/pool sequence. Type a is defined as having small waterfalls,
type b as having turbulent riffles, and type c as having non-turbulent riffles. In general, the upper reaches of rivers in Japan are type Aa, the middle reaches are type Bb, and the lower reaches are type Bc. Aa–Bb and Bb–Bc reach types represent transitional segments. In the Isazu River, Stn. 16.9 was classified as Aa, Stns. 4.7 to 14.5 as Bb, Stns. 2.0 to 4.0 as Bb–Bc, and Stns. 1.1 to 1.6 as Bc (Table 2). In the Yura River, Stns. 12.8 to 17.8 along the main channel were classified as Bc, and Stn. 20.8 was classified as Bb–Bc. In the tributary stations, the reach types varied and were classified as either Bb, B–Bc, or Bc (Table 2).

Stream orders at the sampling stations were determined with a 1:50,000 map published by the Japan Geographical Survey Institute according to the methods of Strahler (1957). Assuming that the channel-network map includes all intermittent and permanent flow lines located in clearly defined valleys, the smallest tributaries are designated order 1. Where two first-order channels join, a channel segment of order 2 is formed; where two order 2 segments join, a segment of order 3 is formed, and so forth (Strahler 1957). In the Isazu River, Stn. 16.9 km was order 1, Stns. 4.7 to 14.5 were order 3, and stations below 4.0 were of order 4 (Table 1). In the Yura River, main stream stations were at order 6 segments, and tributary stations were at orders 1 to 4 (Table 2).

There is one small low-head dam for industrial use (0.5 m height) approximately 2.5 km upstream, and 10 small low-head agricultural dams (0.5–2.2 m height) are located above this dam (Fig. 1). Three large dams (height >15 m) are located in the middle reach of the Yura River at 60.7, 72.0, and 78.5 km from the river mouth (Fig. 1). In the lower reach of the Yura River, one low-head dam (0.5 m height) is located at 48.7 km from the river mouth (Fig. 1).

**Shrimp sampling**

Two types of hand nets were used for sampling shrimp, with mouth widths and mesh sizes of 0.38 m and 1.1 mm, and 0.49 m and 0.1 mm, respectively. The difference in sampling efficiency between the two net types was not considered. Because freshwater shrimp are found in aquatic grass beds, under stones, between crevices, and among fallen leaves (Suzuki et al. 1993), a sweeping method was used for the sampling. In the Isazu River, one to eight sampling blocks 1 m in length were established within 250 m of each sampling station. In the Yura River, sampling was carried out for 10 min by two people or for 20 min by one person in the sampling period from May to June 2007. In the sampling period from December 2008 to January 2009, when sam-

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**Table 2. Summary of sampling stations in the Yura River.**

| Distance from the river mouth (km) | Main stream (M) or Tributaries (T) | Sample seasons | Reach section | Reach type * | Stream order** |
|-----------------------------------|-----------------------------------|----------------|--------------|-------------|---------------|
|                                   |                                   | May–June 2007 | December 2008–January 2009 |             |               |
| 4.4                               | T                                 | ○             | ○            | Lower Bb    | 1             |
| 5.3                               | T                                 | —             | ○            | Lower Bc    | 1             |
| 7.4                               | T                                 | —             | ○            | Lower Bc    | 1             |
| 8.0                               | T                                 | —             | ○            | Lower Bc    | 1             |
| 10.6                              | T                                 | —             | ○            | Lower Bb    | 1             |
| 11.1                              | T                                 | —             | ○            | Lower Bc    | 2             |
| 12.8                              | M                                 | ○             | —            | Estuary Bc  | 6             |
| 13.8                              | T                                 | ○             | ○            | Lower Bc    | 3             |
| 14.6                              | M                                 | ○             | —            | Estuary Bc  | 6             |
| 14.8                              | T                                 | —             | ○            | Lower Bb    | 2             |
| 15.3                              | T                                 | ○             | ○            | Lower Bc    | 3             |
| 16.6                              | M                                 | ○             | —            | Estuary Bc  | 6             |
| 17.8                              | M                                 | ○             | —            | Estuary Bc  | 6             |
| 18.4                              | T                                 | —             | ○            | Lower Bb    | 1             |
| 20.8                              | M                                 | ○             | —            | Lower Bb–Bc | 6             |
| 24.8                              | T                                 | ○             | ○            | Lower Bb    | 4             |
| 27.8                              | T                                 | ○             | ○            | Lower Bc    | 2             |
| 27.9                              | T                                 | —             | ○            | Lower Bb    | 1             |
| 29.3                              | T                                 | —             | ○            | Lower Bb    | 2             |
| 29.8                              | T                                 | —             | ○            | Lower Bc    | 3             |
| 32.9                              | T                                 | ○             | ○            | Lower Bb–Bc | 3             |
| 45.4                              | T                                 | ○             | ○            | Lower Bc    | 3             |
| 49.4                              | T                                 | —             | ○            | Lower Bc    | 3             |

* Based on the Kani’s classification (Kani 1978, Tamada 2011).

** Based on Strahler (1957).
pling was conducted in the tributaries, three sampling blocks each of 5 m in length were established along the channels within 200 m of the junction of the main channel and tributary. All surveys were conducted in the day time.

Water temperature and salinity in the Isazu River and tributaries of the Yura River were measured in the bottom layer of the center channel at each sampling using a Multi Probe System, YSI556MPS or YSI Model 85 (YSI/Nanotech Inc., USA). In the main stream of the Yura River, where the channel center was too deep to enter, water temperature and salinity were measured in the bottom layer 1 m from the riverbank. Measurement of water temperature and salinity at each sampling station was conducted between 10:00 h and 17:00 h.

**Laboratory analysis of samples**

Shrimp were preserved with 10% formalin in the field and observed in the laboratory with a binocular microscope. Identification of each species was made, based on descriptions by Hayashi (1999 a, b, 2000 a–e, 2007). The shrimp were counted and their wet weight was determined. Carapace lengths of some specimens were measured, laterally from the anterior margin of the carapace behind the insertion of the eyestalk to the most distal posterior margin. *Procambarus clarkii* (Girard) was excluded from the analysis, because it is invasive and the distribution pattern of invasive species is considered to be different from the natural distribution of other shrimp species.

**Data analyses**

For sampling in the Yura River from December 2008 to January 2009 and all sampling in the Isazu River, the abundance (ind. m⁻³) and biomass (g m⁻³) of each shrimp species was estimated per 1 m of riverbank by dividing the number of individuals or wet weight of the shrimp by the length of the river bank swept by the net. To enable comparisons of the longitudinal distribution of each shrimp species along the river, shrimp biomass at the Isazu River sampling stations was expressed as the mean annual value.

To show the distribution of each shrimp species in relation to river morphology category, a distribution index (DI) was calculated for each shrimp species and sampling station, determined as the percentage of total biomass of a given species represented by the biomass of that species at each sampling station. Because shrimp densities and quantification methods varied among rivers and seasons, the DI was calculated in three discrete sampling series (Isazu River, Yura River May–June 2007, and Yura River December 2008–January 2009) as

\[ DI(\%) = \frac{B_i \times 100}{\sum B_i} \]

where \( B_i \) is the biomass of the shrimp species caught at station \( i \), and \( \sum B_i \) is the sum of \( B_i \) in a corresponding sampling series. Then we compared the DI to each river morphological category (i.e. reach sections, reach types, and stream orders) of the sampling station. The mean and standard deviation of DI for each shrimp species and each morphological category were examined.

The biomass (g m⁻³) of all the shrimp species measured at each sampling station was compared between the two rivers in the same sampling season. The shrimp biomass data from December 2007 to January 2008 in the Yura River, and in December 2005 (at Stns. 1.6, 2.0, 2.9, 4.0, 4.7) and March 2006 (at Stns. 6.4, 8.1, 12.2, 14.5) in the Isazu River were used for the analyses. Stations where no shrimp were caught were excluded from the comparison. The growth of the shrimp in this period was considered to be negligible, because several previous studies have shown that atyid shrimp show low or no growth at low temperatures (approximately 10°C; see, for example, Oh et al. 2003, Yamahira et al. 2007). A Wilcoxon Mann–Whitney rank sum test was used for data analyses using R version 2.14.1 (R Development Core Team 2011) and coin package for R (Hothorn et al. 2006).

**Results**

**Environmental factors**

In the Isazu River between Stns. 1.6 and 2.0 where annual sampling took place, water temperature decreased from 20°C in October 2005 to 10°C in March 2006, increased to 30°C in August 2006, and then decreased again to 17°C in November 2006 (Fig. 2). At the other sampling stations in the Isazu River, water temperatures showed similar values to those measured at Stns. 1.6 and 2.0 in the corresponding month. In the Yura River, the water temperature ranged from 18.4°C to 22.1°C during sampling from May to June 2007, and from 8.0°C to 15.8°C from December 2008 to January 2009.

Saline water was detected at Stn. 1.1 in the Isazu River, located at the uppermost part of the estuary. The salinity in the bottom layer was 7.2 in August 2006 and 28.8 in September 2006. Salinity was 0 at all stations upstream of Stn.
11 in the Isazu River. In the Yura River, saline water was detected at Stns. 12.8 (1.1), 14.6 (0.8), and 16.6 (0.5) along the main stream. Salinity was 0 at all other main channel and tributary stations in the sampling periods from May to June 2007 and from December 2008 to January 2009.

Species obtained

From the shrimp sampling by net, four species of Atyidae were identified: *Caridina leucosticta* Stimpson, *Caridina serratirostris* De Man, *Paratya improvisa* Kemp, and *Neocaridina denticulata* De Haan. There were two species of Palaemonidae: *Palaemon paucidens* De Haan and *Macrobrachium nipponense* (De Haan). All six species were collected in the Isazu River, and all except *C. serratirostris* were collected in the Yura River.

Seasonal changes in shrimp occurrence

In the annual sampling of the Isazu River, *Caridina leucosticta* dominated at Stn. 1.6, and *Paratya improvisa* at Stn. 2.0, both in terms of abundance and biomass (Fig. 3). Many small individuals of *C. leucosticta* with carapace lengths of 2.1–3.1 mm were recruited to Stn. 1.6 and the abundance and biomass of this species clearly increased in September (Fig. 3). In addition, the recruitment of small individuals of *P. improvisa* in August 2006 resulted in an increase in their abundance and biomass at Stn. 2.0 (Fig. 3). The abundance of *C. leucosticta* at Stn. 1.6 and *P. improvisa* at Stn. 2.0 decreased in March 2006 when temperature decreased to 8.1°C (Figs. 2, 3). However the abundance recovered again in April (Fig. 3). The biomass of *C. leucosticta* at Stn. 1.6 increased from April to June 2006 due to growth and egg incubation by females (Fig. 3). Similarly, the biomass of *P. improvisa* at Stn. 2.0 increased from April to May in 2006 (Fig. 3).

A large number of newly recruited small individuals of *C. leucosticta* and *P. improvisa* strongly influenced shrimp abundance (Fig. 3). The coefficient of variance (CV: standard deviation/mean×100) for monthly abundances of all shrimp was 58.0% at Stn. 1.6 and 166.0% at Stn. 2.0. However, seasonal changes in the biomass of *C. leucosticta* and *P. improvisa* were less varied, and the CV for all shrimp was 39.3% and 50.9% at Stns. 1.6 and 2.0, respectively.

![Species distribution](image_url)
Distribution of freshwater shrimp in two rivers in western Japan

(Fig. 3). Therefore, it is more appropriate to use shrimp biomass, rather than abundance, to compare their longitudinal distribution. In addition, because palaemonids are much heavier and lower in abundance than atyids, biomass is a more appropriate indication of shrimp production at sampling stations than abundance. Consequently, we used the measured biomass to compare the occurrence of shrimp between sampling stations.

*Caridina leucosticta, P. improvisa,* and *Neocaridina denticulata* occurred throughout most months, while the occurrence of *Caridina serratirostris, Macrobrachium nipponense,* and *Palaemon paucidens* was limited in some months. *Caridina serratirostris* was caught in the Isazu River in October 2005 and April and June to September 2006, when the water temperature was 14.7–28.0°C. *Macrobrachium nipponense* occurred in October 2005 and March to May 2006 in the Isazu River, and in May 2007 in the Yura River, when the water temperature was 10.0–21.4°C. *Palaemon paucidens* occurred in March, May, and November 2006 in the Isazu River, and in December 2008 in the Yura River, when the water temperature was 7.8–17.0°C.

Relationships among river morphology, environmental conditions, and shrimp distribution

**Longitudinal distribution**

*Caridina leucosticta* occurred from the brackish area up to the lower reaches. In the Isazu River, this species was distributed from Stns. 1.1 to 4.7, and its biomass was highest at Stn. 1.6 (Fig. 4). In the Yura River, it was distributed from Stns. 12.8 to 32.9 in the sampling period from May to June 2007 and from Stns. 8.0 to 27.9 in the sampling period from December 2008 to January 2009. Biomass was highest at Stn. 13.8 in the Yura River in both seasons (Figs. 5, 6). This species dominated populations at Stns. 1.1, 1.6, 2.5, and 4.0 in the Isazu River (Fig. 4) and at Stns. 11.1–18.4 in the Yura River (Figs. 5, 6).

*Paratyia improvisa* was widely distributed from the lower to middle reaches of the Isazu River, and the biomass was highest at Stn. 4.7 (Fig. 4). This species dominated at Stns. 2.0, 2.9, and 8.1 in the Isazu River (Fig. 4). However, in the Yura River, the biomass of *P. improvisa* was low, and it was sporadically distributed from Stn. 13.8 to 49.4 (Figs. 5, 6). The biomass of this species was high...
only at the uppermost stations (45.5 and 49.4) of the Yura River (Figs. 5, 6).

*Neocaridina denticulata* was found at all stations except Stns. 1.1 and 16.9 in the Isazu River (Fig. 4). This species dominated at both Stns. 4.7 and 12.2 in the Isazu River (Fig. 4), and its biomass was highest at Stn. 4.7. In the Yura River, it was widely distributed from Stns. 10.6 to 49.4 (Figs. 5, 6), dominating at Stns. 17.8–32.9, with its highest biomass at Stn. 29.8 (Figs. 5, 6). *Caridina serratirostris*, which showed lower abundance and biomass compared to other atyids, occurred only at Stns. 1.6 and 2.0 (Fig. 4).

*Macrobrachium nipponense* and *Palaemon paucidens* showed sporadic distribution. *Macrobrachium nipponense* was found at Stns. 1.6, 2.0, and 4.7 in the lower reach of the Isazu River (Fig. 4) and at Stns. 12.8, 13.8, and 15.3 in the brackish estuary of the Yura River (Figs. 5, 6). In the Isazu River, *P. paucidens* occurred at Stn. 1.6 in the lower stream and at Stns. 12.2 and 14.5 the middle stream, and it dominated at Stn. 14.5 (Fig. 4). However in the Yura River, *P. paucidens* was found only at Stn. 29.8 (Figs. 5, 6).

**Altitude**

The altitude (above sea level) of sampling stations along the Isazu River ranged from 2 to 217 m. Along the Yura River, altitude ranged from 0 to 19 m in the sampling period from May to June 2007, and from 0 to 29 m in the sampling period from December 2008 to January 2009. The altitude range of *Caridina leucosticta* was 2–18 m in the Isazu River and 0–9 m in the Yura River. *Paratya impro sola* was widely distributed from 3 to 120 m in the Isazu River, whereas in the Yura River, it occurred at only 19 m in the sampling period from May to June 2007 and at 0 to 29 m in the sampling period from December 2008 to January 2009. *Neocaridina denticulata* was also widely distributed in both rivers, from 3 to 120 m in the Isazu River and in the Yura River from 0 to 19 m in the sampling period from May to June 2007 and from 0 to 29 m in the sampling period from December 2008 to January 2009. *Neocaridina denticulata* was also widely distributed throughout orders 1–4 and 6, while other species had limited distributions among reaches (Fig. 7). Similarly, all species other than *Caridina serratirostris* were found in Bb type reaches (Fig. 7). *Caridina leucosticta* was also collected at a brackish estuary station (Stn. 17.8 in the Yura River), but salinity was zero at the time of collection (Fig. 7). All species occurred in the lower reaches (Fig. 7). In the middle reach, *Paratya improvisa*, *Neocaridina denticulata*, and *Palaemon paucidens* were present, while *C. leucosticta*, *Caridina serratirostris*, and *M. nipponense* were absent (Fig. 7). No shrimp were caught at the upper reach station (Fig. 7).

**Reach type**

In total, one station was located in an Aa type stream reach, 13 were in Bb type reaches, 6 were located in Bb-Bc type reaches, and 15 were in Bc type (Tables 1, 2). No shrimp were found in the Aa type reach, which was the uppermost station of the Isazu River (Fig. 7). All species were present in Bc type reaches, and all species except for *Palaemon paucidens* were found in Bc-Bb type reaches. Similarly, all species other than *Caridina serratirostris* were found in Bb type reaches (Fig. 7). *Caridina leucosticta*, *Paratya improvisa*, *Neocaridina denticulata*, and *Macrobrachium nipponense* were distributed widely across reach type (Fig. 7).

**Stream order**

Eight stations were located in reaches designated order 1, five stations of order 2, ten stations of order 3, seven stations of order 4, and five stations (those along the main stream of the Yura River) of order 6 (Tables 1, 2). There were no stations in fifth order streams. All species were present in fourth-order streams, and all except for *C. serratirostris* were present in third-order streams (Fig. 7). *Caridina leucosticta* and *Neocaridina denticulata* were widely distributed throughout orders 1–4 and 6, while other species had limited distributions among reaches (Fig. 7). *Paratya improvisa* and *Palaemon paucidens* were found in orders 2–4, *Macrobrachium nipponense* in orders 3, 4, and 6, and *Caridina serratirostris* was found in order 4 (Fig. 7).

**Comparison of shrimp biomass between the Isazu and Yura rivers**

Shrimp biomasses measured from December to March at each sampling station ranged from 0.49 to 34.72 g m$^{-1}$ (mean 6.35±0.71) in the Isazu River and from 0.06 to 1.22 g m$^{-1}$ (mean 0.40±0.40) in the Yura River. Shrimp biomasses were significantly higher at stations in the Isazu River than those in the Yura River (Z=3.7662, p=0.00002).

**Discussion**

**Life history of freshwater shrimp**

Six shrimp species were collected in this study. *Carid-
*ina leucosticta* and *Caridina serratirostris* conduct amphidromous migration requiring saline water for larval development (Hamano et al. 2005, Nakahara et al. 2005), while *Paratya improvisa* and *Neocaridina denticulata* are landlocked species and do not require saline water for larval development (Yokoya 1931, Mizue & Iwamoto 1961, Hayashi 2007). Both *Macrobrachium nipponense* and *Palaemon paucidens* have been reported to exist in two population types: one inhabits riverine estuaries and the lower reaches of rivers and has larvae that are believed to migrate to the sea; whereas the other is landlocked, inhabiting inland lakes, ponds, and the upper reaches of rivers (Chow & Fujio 1985, Fidhiany et al. 1988, 1990, 1991, Mashiko 1990, Mashiko & Numachi 1993, 2000). The population of *M. nipponense* of the first type produces large numbers of small eggs with a mean egg volume 0.05 mm$^3$, ...
while the population of the second type produces fewer but larger eggs of mean egg volume 0.06–0.11 mm³ (Mashiko 1990). Although no ovigerous females were caught in the present study, *M. nipponense* in both rivers are thought to conduct amphidromous migration: the habitat of this species corresponds to that of *C. leucosticta* (Figs. 4–6), and it can be assumed that these species have similar climbing abilities. Populations of *P. paucidentes* in the middle reach of the Isazu River (Stns. 12.2, 14.5) and the lower reach of the Yura River are believed to be landlocked, because they were found farther upstream of the typical habitat of *C. leucosticta* in the same sampling series (Figs. 4, 6). However, the population in the lower reach of the Isazu River (Stn. 1.6) is suspected to be only amphidromous.

**Geographical distribution**

Unlike previous studies of shrimp distribution in rivers in Honshu on the Sea of Japan coast (Shimane and Tottori prefectures; Kamita 1970: located west of the collection sites in the present study) and on the Pacific Coast (Kanto district; Usami et al. 2008), the amphidromous species *Macrobrachium formosense* Bate, *Macrobrachium japonicum* (De Haan), *Caridina typus* H. Milne Edwards, and *Caridina multidentata* Stimpson were not seen in the present study. These four species have not been recorded along the eastern coast of the Sea of Japan, including our study sites (Kamita 1970, Ministry of Land, Infrastructure, Transport and Tourism 2004, 2007, Hayashi 2007). Only a small number of *M. formosense* individuals have been recorded in previous surveys in the Isazu River and adjacent rivers in Kyoto Prefecture (Ministry of Land, Infrastructure, Transport and Tourism 2004, 2007). These individuals are thought to be an errant migration population. Therefore, based on previous records (Kamita 1970) and the present study, the eastern limit of the four species’ distribution along the Sea of Japan coast is considered to be Shimane Prefecture for *M. formosense*, *M. japonicum*, and *C. typus*, and Tottori Prefecture for *C. multidentata*.

**Seasonal occurrence**

Life cycle patterns and temperature affected the occurrence of shrimp. The abundance and biomass of *Caridina leucosticta* and *Paratya improvisa* increased in late summer due to the recruitment of juveniles in the Isazu River, displaying the impact of life history. *Caridina leucosticta* and *P. improvisa* decreased in abundance and biomass in March, when the water temperature was lowest, and increased again when the temperature rose, displaying the impact of climate and temperature on shrimp populations. *Macrobrachium nipponense* and *Palaeomon paucidentes* did not occur anywhere at temperatures higher than 22°C, and *M. nipponense* did not occur where the temperature fell below 10°C. It is considered that shrimp are active and crawl out to the surface of their vegetative habitat in moderate temperatures, where they are easily caught; whereas they are inactive and concealed in the substrate when temperatures are suboptimal. Thus, shrimp abundance in this study may have been underestimated when temperatures were outside the optimal range for a given species.

**Relationships among river morphology, environmental conditions, and shrimp distribution**

Two major distribution patterns were related to categories. One group was distributed among lower reaches and brackish estuaries and characterized as amphidromous (*Caridina leucosticta*, *Caridina serratirostris*, and *Macrobrachium nipponense*). The other group was distributed in lower and middle reaches and characterized as landlocked (*Paratya improvisa*, *Neocaridina denticulata*, and *Palaeomon paucidentes*). Previous studies have reported similar distribution patterns (e.g. Shokita 1975, 1979, Suzuki et al. 1993, Usami et al. 2008).

Riverbed gradient, location of dams and natural vertical walls, and the climbing ability of each shrimp species could have determined the distribution of amphidromous shrimp as documented in earlier studies (Shokita 1975, 1979, Miya & Hamano 1988, Suzuki et al. 1993). Potential barriers preventing the upstream migration of shrimp in the Isazu River are three sequential low-head dams placed between Stns. 4.7 and 6.4 (Fig. 1), where the river gradient increases and river discharge decreases due to alluvial fan topography. In the Yura River, a rapid located 40 km from the river mouth is likely to be a barrier for *C. leucosticta*, which migrated longer distances than in the Isazu River because of the generally gentle river gradient with fewer physical obstacles for the shrimp to overcome.

The distribution of each shrimp species in terms of reach types showed similar trends to those observed in previous studies (Shokita 1975, 1979, Miya & Hamano 1988, Niwa & Yokoyama 1993, Usami et al. 2008). However, the migratory species *Caridina serratirostris* and *C. leucosticta*, which were observed within Bc and Bb type reaches in the present study, have been reported in Aa-Bb and Aa type reaches in some short rivers (<10 km) in island and peninsula locations (Shokita 1975, 1979, Usami et al. 2008). The shrimp were able to climb to the upper reaches of these rivers due to the absence of any physical obstacles (natural cascades or dams), as noted by Shokita (1975, 1979).

Lack of salinity tolerance or low salinity tolerance may be one reason why landlocked shrimp were absent from the brackish estuary. Early juveniles of *N. denticulata* in the present study were assumed to have no, or low, salinity tolerance, because early juveniles of several species of the genus *Neocaridina* have been found to die soon after being introduced to seawater (Shokita 1979). Other landlocked shrimp (e.g. *P. improvisa* and *P. paucidentes*) have some salinity tolerance and their larvae develop in seawater (Fidhiany et al. 1991, Kawamura & Akiyama 2010). However, the survival rate of larval *P. improvisa* in seawater (salinity 34) is lower than in brackish water and fresh water (salinity 0–25.5; Kawamura & Akiyama 2010). Similarly, the
survival rate of adult *P. paucidens* (both landlocked and amphidromous populations) also decreases when cultured in seawater, compared to culturing in brackish or fresh water (Fidhiany et al. 1991).

As mentioned above, retention of larvae and postlarvae in the river habitat is an important factor for the survival of landlocked shrimp. Shokita (1979) pointed out that only a few landlocked species inhabit rivers in the Ryukyu Islands because the river courses are too short to sustain landlocked species. In terms of stream order, *N. denticulata* was widely distributed, while *P. paucidens* and *P. improvisa* showed limited distribution in streams of orders 2–4. *Neocaridina denticulata* hatches as a postlarva (first juvenile) without any zoae stage (Mizue & Iwamoto 1961). In contrast, *P. paucidens* and *P. improvisa* hatch as planktonic larvae and spend several zoae stages before developing into juveniles (Yokoya 1931, Fidhiany et al. 1989, Kawamura & Akiyama 2010). These species probably develop in lentic systems (e.g. backwaters) or stream substrates (e.g. aquatic grass beds and the crevices in rocks) where flow is reduced. Their absence from the main channel (order 6) and small tributaries (order 1) of the Yura River is probably explained by the high current velocity and sparse aquatic grass beds along the riverbanks.

Other factors may affect the longitudinal distribution patterns of these shrimp, such as water temperature, predation pressure, food, and refuge availability.

**Comparison of shrimp abundance between the two rivers**

Shrimp biomass in the Isazu River was on mean approximately 16 times higher than that of the Yura River. This difference was probably caused by the difference in coverage of bank vegetation. A previous study reported that shrimp were abundant in rivers with high vegetation coverage (Ideguchi and Yamahira 2004). In the Isazu River, the lush bank vegetation was composed mainly of reeds (*Phragmites* spp.) and willows (*Salix* spp.). In contrast, vegetation coverage in the Yura River was relatively low in both the tributaries and main channel due to disturbances such as saltwater intrusion and water level fluctuation caused by floods. Although there is no information on the predator biomass of the two rivers, potential predators are carnivorous fishes such as largemouth black bass * Micropterus salmoides* (Lacepède), bluegill *Lepomis macrochirus* Rafinesque, and Japanese seabass *Lateolabrax japonicus* (*Cuvier*). The impact of predators is likely to be lower in the Isazu River, where dense vegetation may provide more refuges for the shrimp.

**Conclusions and future perspectives for river ecosystem conservation**

This study shows how riverbed gradients, the location of physical obstacles (e.g. low-head dams), distance from saltwater intrusion, and characteristics of species' life histories are important factors determining the spatial distribution of shrimp. It was also found that river morphology (reach type and stream order) influences the longitudinal distribution of the shrimp. Riverbank structure, especially bank vegetation, may have an important effect on the spatial distribution of shrimp because riverbanks provide the main habitat for freshwater shrimp. Freshwater shrimp species require specific environmental conditions in their habitat. Therefore, detailed information on life history, feeding habits, the favorable environmental conditions for each species, and the impacts of river control structures (such as dams and bank revetments) on migration and retention are important topics that should be considered in future research to effectively conserve these river habitats.

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