DISSERTATION

Regional and local processes in fish assemblage organisation: habitat network in a lowland river and species interactions in headwater streams

魚類群集形成における外部および内部要因：
下流域における水域ネットワークと上流域における種間相互作用

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1. General introduction

Understanding distribution and abundance patterns of organisms has been a central goal in ecology for more than a century (MacArthur and Wilson 1967). Processes of assemblage organisation in a local habitat are roughly classified into regional and local processes (Leibold et al. 2004). Regional processes consist of effects of regional species pools and immigration of species to the local habitat, whereas local processes include species sorting by environmental conditions and biotic interactions operating within the local habitat (Fig. 1.1). Earlier community ecologists have focused on local processes (Jackson et al. 2001). For the last decades, however, increased attention has been paid to regional processes, such as effects of movement of organisms and connectivity among local habitats, owing to the development of metacommunity ecology (Stoffels et al. 2015; Ishiyama et al. 2016). Both processes are important for all communities and their relative contribution changes depending on characteristics of the target local habitat *per se*, its connectivity to surrounding habitats and dispersal characteristics of organisms (Taylor 1997; Cottenie 2005; Ishiyama et al. 2014 Michalet et al. 2015).

River systems are characterised by longitudinal changes in habitat characteristics (Fig 1.2) (Vannote et al. 1980; Church 1992; Allan 1995). Fish assemblage composition responds to such longitudinal environmental gradients (Rahel and Hubert 1991; Torgersen et al. 2006; McGarvey 2010). In temperate regions, fish communities in headwater streams consist of a few cold-water species, and the cold-water species are replaced by warmwater species and species richness increases downstream (Rahel and Hubert 1991; Torgersen et al. 2006). Such downstream increases of species richness are related to downstream increase of productivity

(Horwitz 1978; Cilleros et al. 2017), habitat size (McGarvey 2010) and habitat diversity (Junk et al. 1989; Stein et al. 2014).

Lowland river systems consist of various habitats, such as main channels, tributaries, ponds, wetlands, paddies and ditches, connected by water corridors, forming highly complex networks (Fig. 1.2) (Junk et al. 1989; Ishiyama et al. 2016). In such systems, optimal habitats for fishes are distributed patchily and change depending on life stage (Cooke et al. 2016). Therefore, fish move frequently across aquatic networks in lowland river systems (Junk et al. 1989; Cooke et al. 2016). For example, in Australia, it has been reported that common carp (*Cyprinus carpio*) move from main channels to inundated floodplains for their reproduction after floods, because warm temporal pools in floodplains are suitable for rapid growth of their larvae (King et al. 2003). Also, in lowland river systems, fish assemblages include substantial number of diadromous species (Inoue 2013; Terui and Miyazaki 2016). The abundance and species richness of diadromous species increase with connectivity from the sea (Terui and Miyazaki 2016; Tamario et al. 2019). For example, diadromous fishes, such as *Gymnogobius opperiens*, was distributed mostly in area with < 20 km distance from the sea and their abundance decreased with distance from sea (Miyazaki and Terui 2016). Thus, fish assemblages in lowland river systems consist of substantial numbers of highly mobile species. Frequent movements of fishes can mask effects of biotic interactions and local habitat conditions on fish assemblages. In fact, in lowland river systems, it has often been reported that immigration of external source habitats masked local processes in fish assemblage organisation (Taylor 1997; Uchida and Inoue 2010).

In contrast to lowland river systems, headwater streams are characterised by small and isolated habitats with low productivity (Fig. 1.2) (Erős 2017). Limited resource availability of small habitats can lead to severe competition (e.g. food and habitat space). Also, due to the dendritic structure of river network, local habitats in headwater streams are likely to be more isolated than lowland river systems (Erős 2017). Furthermore, fish assemblage in headwater streams consists of more sedentary species, such as cottids and salmonids, than fishes in lowland river systems (Erős 2017). For example, Natsumeda (2003) reported that most individuals of fluvial sculpin moved only < 100m during a seven-month survey period. Also, juvenile steelhead rarely disperse from their local habitat units (5 – 15 m) (e.g. pool, riffle, run) during a three-month survey period (Anderson and Kennedy 2020). In such systems with lower resource availability and lower movement rates, fish assemblage organisation can strongly reflect consequences of biotic interactions within local habitats. In fact, for stream dwelling salmonids in headwater streams, displacement of native species by introduced species (competitive exclusion) has often been reported (McHugh and Budy 2005; McMahon et al. 2007; Inoue et al. in press). Overall, in headwater streams, effects of local processes (e.g. biotic interactions) on fish assemblage organisation can override those of regional processes.

In this dissertation, I explored mechanisms underlying fish assemblage organisation in headwater streams and a lowland river system. In the lowland river system, I focus on fish movement across a channel network and its effects on local fish assemblages, using a braided river (chapter 2). In headwater streams, I focus on biotic interactions causing longitudinal replacement of salmonids (chapter 3).

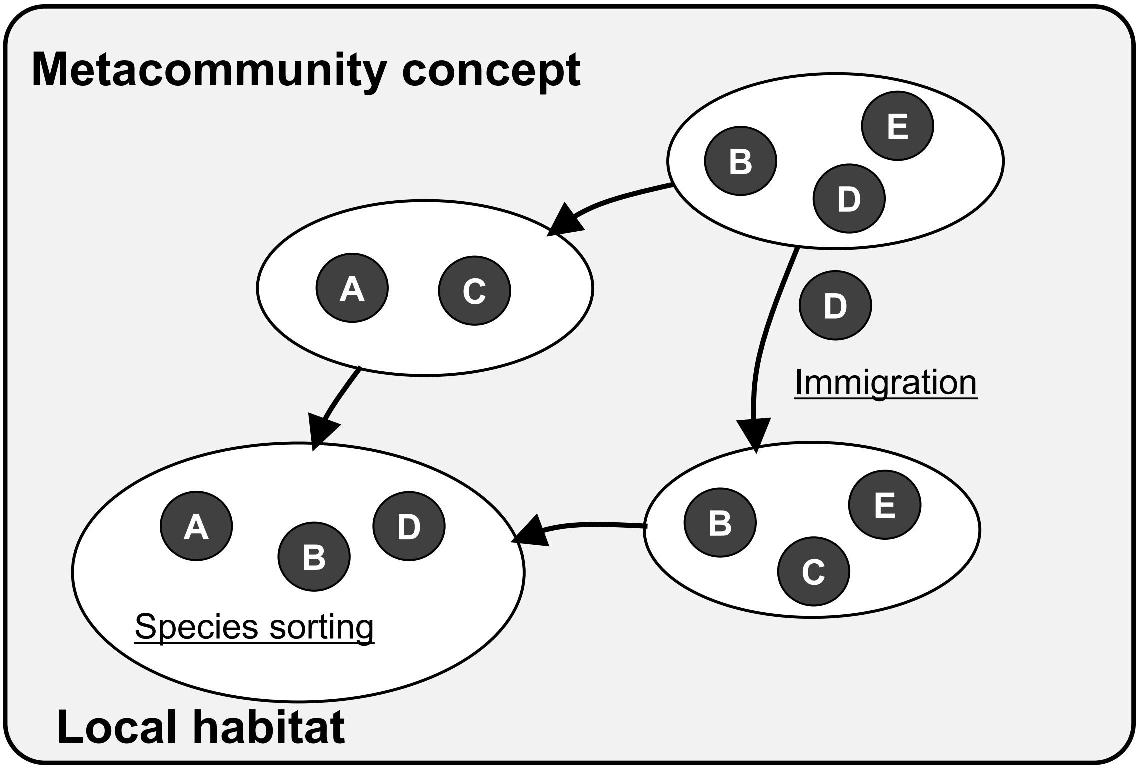

Fig. 1.1 Regional and local processes in metacommunity concept

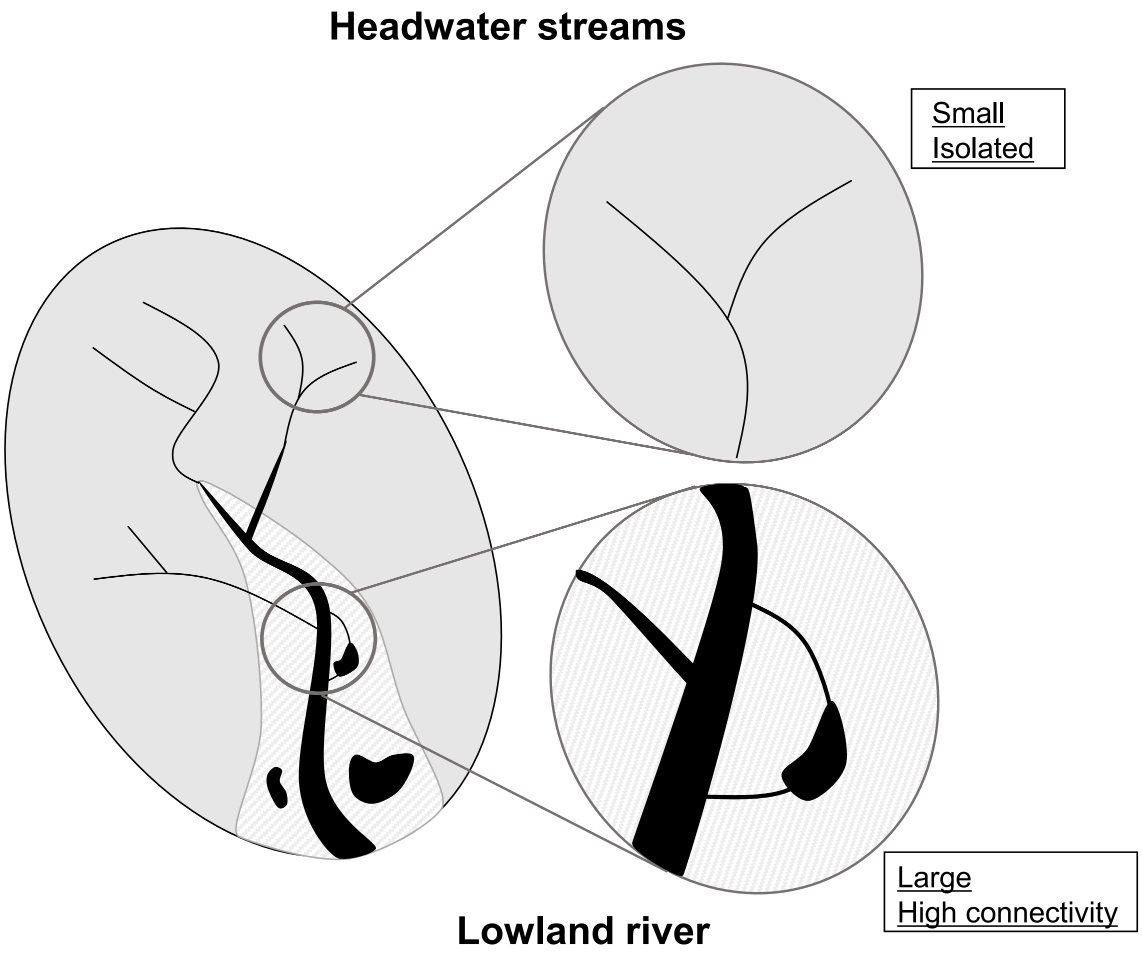

Fig. 1.2 Concept of longitudinal changes in habitat characteristics in river systems

2. Effects of fish movement in lowland freshwater systems

Lowland river systems are characterised by high productivity, spatiotemporal environmental variability and diverse biota (Amoros and Bornette 2002; Tockner and Stanford 2002). These systems consist of various habitats, such as main channels, tributaries, ponds, wetlands, paddies and ditches (Ishiyama et al. 2016). In such river systems, optimal habitats for fishes would be distributed in patches and their distribution can change depending on season and ontogeny (Cooke et al. 2016), suggesting that movement among habitats would provide fish with benefits on their survival and growth (King et al. 2003; Shao et al. 2019). Also, it has often been reported that spawners move from main channels to floodplains for reproduction (King et al. 2003). Positive relationships between species richness of fish and habitat connectivity have often been observed (Taylor 1997; Uchida and Inoue 2010; Ishiyama et al. 2014). These positive relationships suggest that habitat connectivity and fish movement across river networks would be an important factor affecting fish assemblage organisation in lowland river systems. Therefore, across their life stages and seasons, assessments of fish movement among habitats would facilitate better understanding fish assemblage organisation.

When fish move through lowland river network systems, individuals have to select their way at each junction (i.e. confluence) in the network. At a confluence of two channels between which water characteristics (e.g. temperature, turbidity) differ distinctly, fish would select either of the two on the basis of the differences. It has often been reported that fish aggregate in streams or local habitat patches with unique thermal regimes, like aggregation in cold or warm spring-fed water (Moss 1985; Ebersole et al.

2001; Koizumi et al. 2017). An outdoor-channel experiment examining effects of turbid water (suspended silt) on a stream fish (ayu: *Plecoglossus altivelis*) demonstrated that fish moved from a turbid stream to an adjacent non-turbid, clear stream, which resulted in inter-stream differences in fish density (Mori et al. 2018). These studies of fish behaviour suggest that fish may respond to environmental differences at a confluence of two channels and their response would be species-specific. However, channel selection by fish at confluences during their movement has rarely been examined in the field. Such information on channel selection in a habitat network would be important for a better understanding of assemblage organisation in local habitats where regional processes have prominent effects, because channel selection at each confluence during movement would be reflected in the spatial variations in fish assemblage compositions among the local habitats in the network. Although the importance of regional processes in lowland freshwater systems has been established (Lasne et al. 2007; Bouvier et al. 2009; Stoffels et al. 2015), effects of route selection by fish during inter-habitat movement have received little consideration. This is probably because such network systems are usually so extensive and complex that it is difficult to assess the effects on local fish assemblages.

Braided reaches, which are formed in rivers with high sediment loads, consist of networks of multiple channels that often have various environmental conditions (Van der Nat et al. 2003; Gray and Harding 2009). Braided channels are usually unstable; the form and arrangement of channel networks are frequently altered by the movement of coarse sediment due to high flow events (Malard et al. 2006). In a braided reach, therefore, many confluences of various pairs of stream channels can occur spatially and temporally within a relatively limited area and a short period. Such a unique feature of braided channels provides a good opportunity to examine channel selection by fish. Furthermore, braided rivers contain a diverse array of habitats, such as the main channel, side braid, backwater, and spring stream within a relatively limited area (Van der Nat et al. 2003; Gray and Harding 2009). Therefore, braided rivers are useful to survey seasonal movement across different habitat types and examine effects of both local and regional factors affecting local assemblages.

In this chapter, I focused on effects of fish movement on assemblage organisation, using a braided river. First, I examined effects of channel selection during movement on local fish assemblage (chapter 2-1). Next, I explored seasonal movement of fishes at a confluence of surface-water and groundwater channels (chapter 2-2). Finally, I conclude with discussion of effects of habitat connectivity and fish movement on fish assemblage organisations (chapter 2-3).

2-1. Route selection by fish during post-spate movement in a braided river: a potential effect on local assemblages

2-1-1. Introduction

Fish assemblage composition in a local habitat, such as a stream reach and a floodplain pond, is largely determined by the species that migrate into the local habitat (i.e. immigration or regional processes) and the species that have successfully settled (i.e. extinction or local processes) (Rodríguez and Lewis 1994; Magnuson et al. 1998; Stoffels et al. 2015). Although earlier studies tended to focus on local processes (e.g. biotic interactions, local habitat conditions) (Rahel 1984; Capone and Kushlan 1991; Rodríguez and Lewis 1997), the importance of regional processes (e.g. dispersal and inter-habitat movement) is now well recognised, owing to the development of metacommunity ecology (Bouvier et al. 2009; Jacobson and Peres-Neto 2010; Uchida and Inoue 2010; Stoffels et al. 2015). In lowland freshwater systems, several studies have shown that species richness or composition is more strongly affected by the distance or connectivity to surrounding habitats than by local habitat factors (Bouvier et al. 2009; Uchida and Inoue 2010), suggesting overriding effects of dispersal or inter-habitat movement in determining the assemblage composition in those systems.

In general, lowland freshwater systems are complex networks of various aquatic habitats such as rivers and their tributaries, floodplain ponds, wetlands, and paddies, which are connected by watercourses with each other (Ishiyama et al. 2016). When fish move through such a network system, individuals have to select their way at each junction (i.e. confluence) in the network. At a confluence of two channels between which water characteristics (e.g. temperature and turbidity) differ distinctly, fish would select either of the two on the basis of the differences. It has often been reported that fish aggregate in streams or local habitat patches with unique thermal regimes, like aggregation in cold or warm spring-fed water (Moss 1985; Ebersole et al. 2001; Koizumi et al. 2017). An outdoor-channel experiment examining the effects of turbid water (suspended silt) on a stream fish (ayu: *Plecoglossus altivelis*) demonstrated that fish moved from a turbid stream to an adjacent non-turbid, clear stream, which resulted in inter-stream differences in fish density (Mori et al. 2018). These studies of fish behaviour suggest that fish may respond to environmental differences at a confluence of two channels and their response would be species-specific. However, channel selection by fish at confluences during their movement has rarely been examined in the field. Such information on channel selection in a habitat network would be important for a better understanding of assemblage organization in local habitats where regional processes have prominent effects because channel selection at each confluence during movement would be reflected in the spatial variations in fish assemblage compositions among the local habitats in the network. Although the importance of regional processes in lowland freshwater systems has been established (Lasne et al. 2007; Bouvier et al. 2009; Stoffels et al. 2015), effects of route selection by fish during inter-habitat movement have received little consideration. This is probably because such network systems are usually so extensive and complex that it is difficult to assess the effects on local fish assemblages.

Braided reaches, which are formed in rivers with high sediment loads, consist of networks of multiple channels that often have various environmental conditions (Van der Nat et al. 2003; Gray and Harding 2009). Braided channels are usually unstable; the form and arrangement of channel networks are frequently altered by the movement of coarse sediment due to high flow events (Malard et al. 2006). In a braided reach, therefore, many confluences of various pairs of stream channels can occur spatially and temporally within a relatively limited area and a short period. Such a unique feature of braided channels provides a good opportunity to examine channel selection by fish. For example, after high flow events, which generally elicit fish movement (Lyon et al. 2010; Marshall et al. 2016), fish individuals would have to select a channel at each confluence during their movement over the channel network.

Braided reaches also contain a diverse array of habitats, such as the main channel, side braid, backwater, and spring stream, within a relatively limited area (Van der Nat et al. 2003; Gray and Harding 2009). Therefore, it is useful to examine the effects of both local habitat factors and habitat connectivity on local assemblages (Taylor 1997; Arscott et al. 2005). That is, braided channels are an ideal system for examining channel selection by fish and its consequences on local assemblage composition. In this study, I examined channel selection by fish during their movement after high-flow events in a braided river. I also examined whether spatial variations in local fish assemblages in the braided channel network reflected species-specific differences/similarities in their channel selection.

2-1-2. Materials and methods

Study area

The study was conducted in the Shigenobu River (catchment area: 445 km^2; main stem length: 36 km) on Shikoku Island, Japan (Fig. 2-1.1). The catchment receives an annual precipitation of ca. 1300 mm, with a rainy season spanning early summer to fall. This river has formed a large alluvial fan, owing to high sediment yield in its upper reaches. On the alluvial fan, a braided channel is developed (bankfull width: ca. 300 m), and the river flow from the upper reaches sinks into thick alluvial deposits at the upper side of the alluvial fan (i.e. ephemeral flow). On its downstream side, the subsurface water seeps from the deposits, and such seepage-fed streams form the braided channel. In this seepage-dominated braided reach, rainfall-derived runoff is also delivered from upstream during and after the precipitation events. In such situations, the stream channels of the braided reach are broadly categorised as seepage- or runoff-dominated channels. In general, runoff-dominated water is more turbid than seepage-dominated water, because runoff entrains fine sediments from the land surface (e.g. Malard et al. 2006). Furthermore, the temperature of runoff water differs distinctly from that of seepage water, with the former being higher than the latter in summer and *vice versa* in winter (Caissie 2006). As a result, during and after high-flow events, several confluences of two channels that differ in flow volume, thermal condition, and water quality, are repeatedly formed in the braided reach. Using these confluences formed after summer high-flow events, I examined the characteristics of the channels selected by fishes. I also analysed correlative patterns among the abundances of assemblage members and local habitat variables in study sites established in the channel network to examine whether fish assemblage composition reflected their channel selection. In this braided reach, fish fauna is dominated by four species, *Opsariichthys platypus* (pale chub), *Rhynchocypris oxcycephala* (fat minnow), *Cobitis* sp. BIWAE type A (spined loach) and *Rhinogobius nagoyae* (freshwater goby).

Channel selection by fish

Field survey

A channel-selection survey was conducted at confluences formed within a 2.5 km stretch of the braided reach (Fig. 2-1.1) after four summer high-flow events that occurred on 20 June, 7 July, and 7 and 10 September 2018 (Fig. 2-1.2). In two channels forming each confluence, fish moving upstream were captured using fyke nets (Fig. 2-1.1), and the channel in which more fish were captured was assumed to be ‘selected’ (see below for details). At each channel, a fyke net with double wing (4 mm mesh, 2 or 3 m wing, depending on the channel width) was set at ca. 2 m upstream from the confluence, blocking the entire channel (additional block nets were used at large channels). The fyke nets were set for a whole day and night, or half a day, depending on flow conditions (see below), with the fyke traps being checked at around 6:00 and 18:00 hours. Fish captured in the traps were identified, counted, and released on the upstream side of the trap (the presumed direction of movement), and expressed as number per half day.

During the survey periods (i.e. falling limb of the hydrograph: Fig. 2-1.2), branching patterns of the channel network and flow conditions were always changing according to declining water levels. For example, one day, wetted width, water depth and current velocity of two channels at one confluence were too large and too fast to set fyke nets, and then flow conditions of the two channels became adequate for the fyke-net setting on the next day, but water depth became too shallow to set on the following day. Thus, the occurrence of confluences adequate for the survey was highly variable in space and time after high flow events, and I set fyke nets as many as possible during the summer. Consequently, I surveyed at 82 confluences in total during the four post-spate periods (Fig. 2-1.2).

At each channel of the confluences, the flow volume, water temperature, water depth, current velocity, and turbidity were measured to characterise the environmental conditions of the channel. Water temperature was recorded at 10-minute intervals during fish sampling with a data logger (HOBO Temp, Onset) set at each fyke trap, and represented by their average value. Wetted width, water depth, and current velocity of each channel were measured using a transect set at approximately 1 m upstream from the confluence, and flow volume was estimated. At 5–10 equidistant points along the transect, the water depth (cm) and current velocity (cm s^{-1}) at 0.6 depth were measured using a portable current metre (CKK-VR301, KENEK), and the mean depth and mean velocity for each channel were calculated. The flow volume of each channel was calculated on the basis of the depths and velocities measured on the transect (see Gore 1996). The water turbidity (NTU) in each channel was measured at the centre of the flow using a portable water quality metre (U-53, HORIBA). These measurements (depth, velocity, and turbidity) were conducted at the beginning of fish sampling. The study channels varied from 1 to 19 m in wetted width and from 18 to 29 °C in water temperature (Table 2-1.1). The maximum difference between paired channels was 16 m in wetted width and 7 °C in water temperature (Fig. 2-1.3; see Fig. S2-1.2 for other variables).

Data analysis for channel selection

Although 24 species were captured during the study, the four dominant species, pale chub, fat minnow, spined loach and freshwater goby, comprised more than 90% (Table S2-1.1), and the other species were sporadically captured at a few sites. Therefore, the four dominant species were used for the analysis. Their movement in the study area was highly variable and unpredictable in space and time. Therefore, although I surveyed at 82 confluences in total, sufficient numbers of individuals were not always captured. Although fat minnow was captured at all of the 82 confluences, pale chub, spined loach, and freshwater goby were captured at 45, 68, and 46 confluences, respectively. Furthermore, there were many cases where the number of captured individuals was too small to judge which channel was selected (e.g. the number of fish captured by paired channels were 0 versus 1) (Fig. S2-1.1). Therefore, I used a binomial test to omit such cases. For each species at each site (confluence), the binomial test was performed to determine whether the difference in the number of captured fish between two channels at a confluence was more than expected by chance ($P = q = 0.50$, alpha = 0.05). As a result, the binomial test was significant ($P < 0.05$) for 14, 59, 10, and 7 confluences for pale chub, fat minnow, spined loach and freshwater goby, respectively (Characteristics of these confluences with significant differences and others are shown in Fig. S2-1.2). In these cases, I assumed that the channel in which more fish were captured was ‘selected’, and these cases were used for further analysis; however, freshwater goby was omitted from the analysis because of the small sample size ($N = 7$ pairs). In these data sets, the number of individuals of pale chub, fat minnow, and spined loach captured ranged from 0 to 99, 0 to 141, and 0 to 231 (per trap per half day), with the difference between paired channels being 17 to 83, 6 to 131, and 9 to 231, respectively. To examine differences in the environmental variables between selected and unselected channels, I compared flow volume, mean water temperature, mean depth, mean velocity, and turbidity between selected and unselected channels using a paired *t*-test. Flow volume, mean depth, mean velocity, and turbidity were $\log_{10}$-transformed before the analysis.

Correlative patterns

Fish and habitat data

I examined the relationships between local densities of fish assemblage members and local habitat variables, using fish and habitat data in the study area obtained in the summer of 1999, 2009, and 2012. These data were gathered for other purposes; however, fish and habitat surveys were conducted in a similar manner. Several study reaches were established within the 2.5 km stretch of the braided channel network (Fig. 2-1.1); the length of the study reaches was 49–70 m ($N = 7$), 11-80 m ($N = 15$), and 24–40 m ($N = 8$) in 1999, 2009 and 2012, respectively, depending on the stream size. The density of each fish species and some habitat variables were quantified in each study reach.

Fish density data for 1999 and 2012 were based on electrofishing, whereas those for 2009 were obtained by underwater visual counts. In the electrofishing survey in 1999 and 2012, three removal passes were made in each study reach using an electrofishing unit (Model 12 Backpack Electrofisher, Smith-Root Inc.), and the captured fish were identified to species, counted, and released. The density of each species was calculated by dividing the total number of individuals caught by the three passes by the area of the study reach. Underwater fish counts in 2009 were conducted using transects. In each study reach, 5 or 6 belt transects (1 m width) perpendicular to the flow were established, snorkelling was conducted along the transects, and the number of each fish species encountered within the belt was recorded. The density of each species was expressed as the number of individuals per transect area. This underwater visual survey was conducted under low flow conditions (i.e. high water clarity) between high flow events in July, and the four target species (i.e. dominant species: pale chub, fat minnow, spined loach, and freshwater goby) are diurnally active. Therefore, the underwater visual survey is an effective method to quantify among-site variations in fish abundance (e.g. Uchida and Inoue 2010). The fish surveys in 1999 and 2012 were also conducted under low flow conditions between high-flow events in July and August–September, respectively (Fig. S2-1.3).

The summer maximum water temperature, wetted channel width, water depth, substrate, and cover were quantified as local habitat variables in each study reach, although the substrate was not surveyed in 2009. The maximum water temperature was recorded using a maximum-minimum thermometer at each study reach for 4–7 days in mid- to late July 1999, for 3 days in mid-July 2009, and for 40 days from late July to the end of August 2012. Wetted width, water depth, and substrate were quantified using a transect method. In each study reach, 5–19 equally spaced transects were established, depending on the stream size. Wetted width and the maximum depth at each transect were measured, and their mean values were calculated. Substrate was assessed at seven equidistant points along each transect in 1999 and 2012. The substrate type within a 900 cm^2 (30 cm × 30 cm) area at each of the seven points was coded in order of coarseness as follows: 1 = bedrock, 2 = sand (dominant particle size < 2 mm), 3 = gravel (2–16 mm), 4 = pebble (17–64 mm), 5 = cobble (65–256 mm), 6 = boulder (> 256 mm). The mean and standard deviation of these coded values were used to express the substrate coarseness and heterogeneity, respectively (Bain et al. 1985). Instream woody debris, concrete structures (e.g. tetrapods), aquatic macrophytes, and overhanging terrestrial vegetation (instream or within 40 cm of the water surface) were considered cover materials. The length and several widths of each cover material within each study reach were measured, and the percentages of the occupied area within the wetted water surface was calculated to represent cover abundance.

Data analysis for correlative patterns

The four dominant species, pale chub, fat minnow, spined loach, and freshwater goby, were examined. The relationships of the density of each species to habitat variables and the density of other species were examined using simple correlation analysis. I expected that 1) when the density of a species was largely controlled by local habitat factors, the density would be most strongly correlated with a local habitat variable, 2) when the density was largely controlled by interspecific competition with another species, strong negative correlations would be found between densities of some species, and 3) when regional processes (e.g. inter-habitat movement) or stochastic factors have overriding effects on the density, both of the above correlations would be unclear. In addition, when inter-habitat movement has overriding effects and channel selection during movement is influential, correlations among the densities of the four species in the study reaches would reflect species-specific differences/similarities in channel selection. For example, if two species have a similar channel preference, a strong correlation between the densities of the two species would be found. This analysis was conducted separately for each year. Fish densities, wetted width, and water depth were $\log_{10}$–transformed, while the percentage of cover area was arcsine–square–root transformed to standardise variance and improve normality.

2-1-3. Results

Channel selection

Paired *t*-tests showed that environmental characteristics significantly differed between selected and unselected channels for fat minnow and spined loach, but not for pale chub (Fig. 2-1.4, Table S2-1.2). Regarding pale chub, although the difference was not statistically significant ($P = 0.099$), the water temperature of the channels selected by the pale chub was always higher than, or similar (±1°C) to that of respective opponent channels (Fig. 2-1.4). Channels selected by fat minnow had significantly lower flow volumes and lower current velocities than unselected channels (Fig. 2-1.4). The results for spined loach were similar to those for fat minnow. Channels selected by spined loach were characterised by significantly shallower depth, lower flow volume and higher water temperature (Fig. 2-1.4).

Correlative patterns

Correlation analysis showed that no consistent relationships were found between the fish density and local habitat variables, whereas positive correlations between the densities of fat minnow and spined loach were consistently found across the three different years (Table 2-1.2, Fig. 2-1.5). The density of pale chub was positively correlated with the water temperature and the density of freshwater goby in 2009. However, no significant correlation was found in the other years. The density of fat minnow was most strongly correlated with that of spined loach in both 1999 and 2009. In 2012, although the positive correlation with spined loach was not the strongest, it exhibited a high coefficient value ($r = 0.78$). Regarding spined loach density, the positive correlation with fat minnow density was the strongest in every year. The density of freshwater goby was positively correlated with that of pale chub in 2009 and with substrate heterogeneity in 2012; no significant correlation was found in 1999.

2-1-4. Discussion

The results of channel-selection survey showed that environmental characteristics differed between the selected and unselected channels for fat minnow and spined loach. The channels selected by these two species were similarly characterised by a lower flow volume. The analysis of the correlative patterns among local fish densities and habitat variables using data from three different years revealed that the most consistent pattern was strong positive correlations between the densities of fat minnow and spined loach, which were found to have similar channel preferences in the channel-selection survey. These results suggest that the fish assemblage composition of local habitats in the braided channel network of the study river reflected, at least in part, species-specific channel preference during movement at high-flow events.

The channel network of the braided reach consisted of seepage-fed and run-off streams. Therefore, I had expected some responses of fishes to water temperature and/or turbidity. For example, pale chub is a common warm water species distributed in the middle to lower reaches of rivers in southwestern Japan (warm-temperate climate) (Hosoya 2015). Therefore, I expected that the pale chub would avoid colder, seepage-fed water. Although not statistically significant, pale chub appeared to prefer channels with higher water temperature, as expected (Fig. 2-1.4). In contrast to pale chub, fat minnow usually inhabits the upper reaches (Fujita 2015a), and can be regarded as a -cold-water species as it often coexists with salmonids in headwater streams (Inoue et al. 2013). I consider that the fat minnow population in the study reach, which is located at the downstream margin of the distribution range of this species, is maintained owing to cool, seepage-fed water. Therefore, I expected that fat minnow would select channels with lower water temperature. However, this effect of water temperature was not detected. Instead, the channels selected by fat minnow were characterised by lower flow volume and lower current velocity (Fig. 2-1.4). A similar pattern in channel selection was detected for spined loach. The channels selected by spined loach had lower flow volume and shallower depth than the unselected channels (Fig. 2-1.4). Channel selection by the two species was similar in that they tended to avoid stronger currents. Such a pattern in channel selection at confluences may be related to their swimming ability.

Simple correlation analysis on local assemblages indicate that no local habitat variables had a consistent effect across the three different years. In addition, no negative correlations were found among the densities of the four species. These results suggest that regional processes or stochastic factors have overriding effects on the density of each species in my braided channel network, compared to local processes. Given the unstable nature of the braided channels, the local fish density in my study area can be largely affected by stochastic factors. Nevertheless, strong positive correlations between the densities of fat minnow and spined loach were consistently found across the three different summers (Fig. 2-1.5, Table 2-1.2). This could be due to the effect of an unmeasured local habitat factor that works in a similar manner for both species, or due to their similar channel preference during movement, as revealed by channel-selection survey. The two species distinctly differ in body morphology, behaviour, and habitat use. Spined loach is a typical benthic fish, preferring sandy substrates in the warm water of the middle to lower reaches (Nakajima and Uchiyama 2017), while fat minnow is a water-column fish inhabiting cool water in the upper reaches (Fujita 2015a). It is difficult to find a local habitat factor that similarly affects the densities of the two species with such different characteristics. In the study area, high-flow events frequently occur in summer (Fig. 2-1.2), and fish would move actively or passively during and after high-flow events (e.g. refuge seeking, downstream displacement, return after displacement). The consistent strong correlations between the densities of fat minnow and spined loach are most likely due to their similar channel preference during their movement.

Overall, my results suggest that, in the braided channel network, fish assemblage composition of local habitats is controlled predominately by regional processes (i.e. inter-habitat movement), and that channel selection (route selection) during movement can be an important factor in local assemblage organization. Braided rivers are highly dynamic systems, with multiple channels becoming connected and disconnected, depending on changes in the water level (Van der Nat et al. 2003). At high flow events, fish movement over a channel network is facilitated (Lyon et al. 2010; Marshall et al. 2016) and local assemblages would be shuffled. Therefore, it is reasonable that the analysis of correlative patterns in the three summers (rainy season) detected no effects of local factors, probably owing to the overwhelming effects of inter-habitat movement facilitated by frequent high-flow events. An important suggestion from this study is that, in situations where dispersal or inter-habitat movement has overriding effects on local assemblage organization, the effects of route selection during dispersal or movement are non-negligible. This view may be applied to more extensive systems similar to braided channel networks, e.g. such as river-floodplain systems. In lowland alluvial plains, freshwater systems consist of various aquatic habitats, such as river mainstems, tributaries and distributaries, floodplain ponds, paddies, and their associated ditches (Ishiyama et al. 2016), exhibiting a web-like structure. Fish species diversity, composition, and population stability in floodplain habitats around a river are often strongly affected by regional processes (Lasne et al. 2007; Sullivan and Watzin 2009; Uchida and Inoue 2010; Stoffels et al. 2015). Therefore, consideration of route selection by fish during dispersal or movement can contribute to a better understanding of assemblage organization in such habitats.

Rivers and their associated aquatic habitats are characterised by network structure (Benda et al. 2004; Altermatt 2013), with local habitats (e.g. river reaches) connected at junctions (i.e. confluences). During the last few decades, increased attention has been paid to effects of network structure (Benda et al. 2004; Grant et al. 2007; Terui et al. 2018) and confluences *per se* (Rice et al. 2001; Czeglédi et al. 2016; Boddy et al. 2019) on riverine geomorphology (habitat structure) and assemblage organization. An important role of confluences in assemblage organization is to affect the dispersal processes of aquatic organisms (Czeglédi et al. 2016; Boddy et al. 2019), although direct surveys of species sorting at confluences have rarely been conducted. As channel-selection survey shows, confluences can sort dispersers via species-specific responses to between-channel differences in environmental conditions. Therefore, route selection (e.g. selection of tributaries) by fish at confluences during their dispersal or movement can greatly contribute to producing variations in assemblage composition among local habitats (e.g. between a tributary and the mainstem, and among tributaries). A similar suggestion was proposed by Mori et al. (2018), who experimentally showed avoidance of turbid waters by a stream fish (ayu) at a confluence of artificial channels. Their results suggested that the inter-stream movement caused by such avoidance behaviour results in between-tributaries differences in ayu density. A dendritic or web-like structure is a unique property of inland freshwater systems. Unlike animals in marine and terrestrial systems (e.g. marine fishes, birds, and insects), the dispersal and movement of freshwater fish are restricted to a network of waterways. Therefore, route selection by fish, or the sorting role of confluences, is a notable factor determining the assemblage composition of freshwater fish.

Table 2-1.1. General descriptions of the study channels for the channel selection survey

	Mean ± SD	Range
Water temperature (˚C)	22.3 ± 2.3	17.7-28.6
Flow volume ($m^3 \cdot s^{-1}$)	0.338 ± 0.289	0.003-1.540
Wetted width (m)	6.9 ± 3.2	0.9-18.8
Mean depth (cm)	14.5 ± 7.0	2.9-34.6
Mean velocity ($cm \cdot s^{-1}$)	31.0 ± 17.0	3.8-82.8
Turbidity (NTU)	2.4 ± 3.3	0.0-17.8

Table 2-1.2. Correlation coefficients (Pearson's *r*) of the density of each species with local habitat variables and other species' density (*N*=7, 15, 8 in 1999, 2009, 2012, respectively)

	Pale chub						Fat minnow						Spined loach						Freshwater goby					
	1999		2009		2012		1999		2009		2012		1999		2009		2012		1999		2009		2012	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Environmental variable																								
Width	0.30	(0.473)	0.45	(0.093)	-0.29	(0.533)	0.17	(0.681)	-0.70	(0.004)	-0.81	(0.027)	0.57	(0.138)	-0.69	(0.005)	-0.52	(0.235)	-0.54	(0.170)	0.23	(0.404)	0.24	(0.597)
Temperature	0.08	(0.853)	0.66	(0.008)	0.03	(0.953)	0.30	(0.468)	0.16	(0.574)	-0.90	(0.006)	0.00	(0.995)	-0.01	(0.723)	-0.51	(0.238)	0.35	(0.389)	0.17	(0.546)	-0.03	(0.942)
Depth	0.10	(0.809)	0.29	(0.289)	0.25	(0.596)	0.31	(0.458)	0.33	(0.234)	0.41	(0.359)	0.47	(0.237)	0.03	(0.909)	0.31	(0.504)	-0.28	(0.506)	0.00	(1.000)	0.37	(0.420)
Cover area	-0.33	(0.425)	-0.39	(0.156)	0.59	(0.167)	-0.37	(0.373)	0.72	(0.002)	0.57	(0.180)	-0.66	(0.077)	0.63	(0.013)	0.51	(0.247)	0.32	(0.447)	-0.30	(0.279)	-0.11	(0.814)
Substrate coarseness	-0.05	(0.906)			0.05	(0.918)	0.49	(0.215)			0.43	(0.340)	0.48	(0.228)			0.01	(0.978)	-0.30	(0.473)			-0.58	(0.173)
Substrate heterogeneity	0.22	(0.606)			0.09	(0.843)	0.19	(0.646)			-0.06	(0.893)	0.33	(0.432)			0.12	(0.795)	-0.07	(0.872)			0.79	(0.033)
Fish density																								
Pale chub							0.61	(0.112)	0.04	(0.878)	0.29	(0.526)	0.61	(0.112)	-0.22	(0.474)	0.49	(0.269)	0.41	(0.307)	0.65	(0.009)	0.00	(0.996)
Fat minnow	0.61	(0.112)	0.04	(0.878)	0.29	(0.526)							0.79	(0.002)	0.84	(<0.001)	0.78	(0.038)	0.35	(0.396)	0.06	(0.830)	0.28	(0.548)
Spined loach	0.61	(0.112)	-0.22	(0.474)	0.49	(0.269)	0.79	(0.002)	0.84	(<0.001)	0.78	(0.038)							-0.20	(0.644)	-0.10	(0.721)	0.55	(0.203)
Freshwater goby	0.41	(0.307)	0.65	(0.009)	0.00	(0.996)	0.35	(0.396)	0.06	(0.830)	0.28	(0.548)	-0.20	(0.644)	-0.10	(0.721)	0.55	(0.203)						

Significant correlations ($P < 0.05$) are underlined.

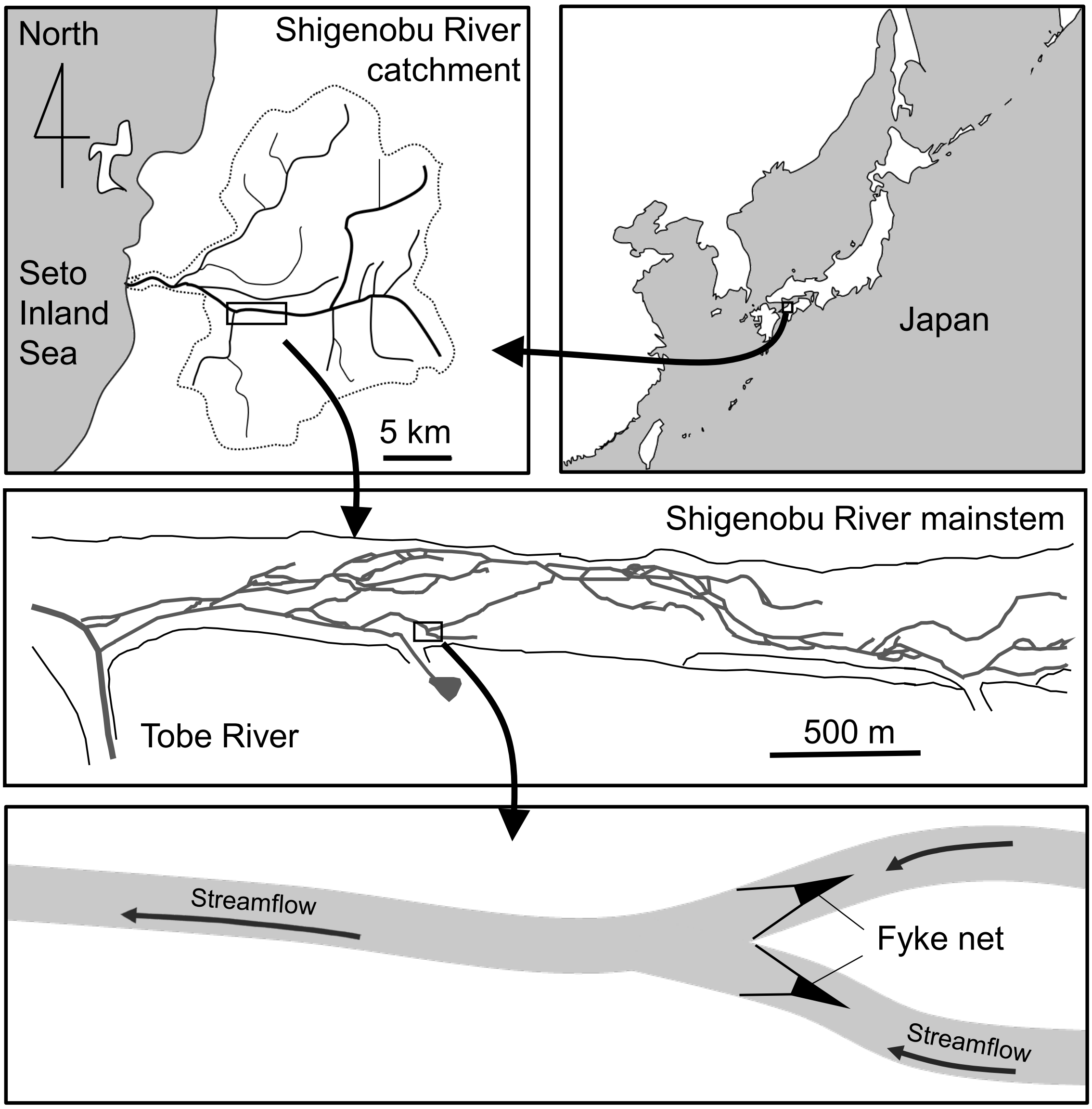

Fig. 2-1.1. Location (upper) and map (middle) of the study area, a braided reach of the Shigenobu River, with a schematic illustration of fyke net configuration (lower).

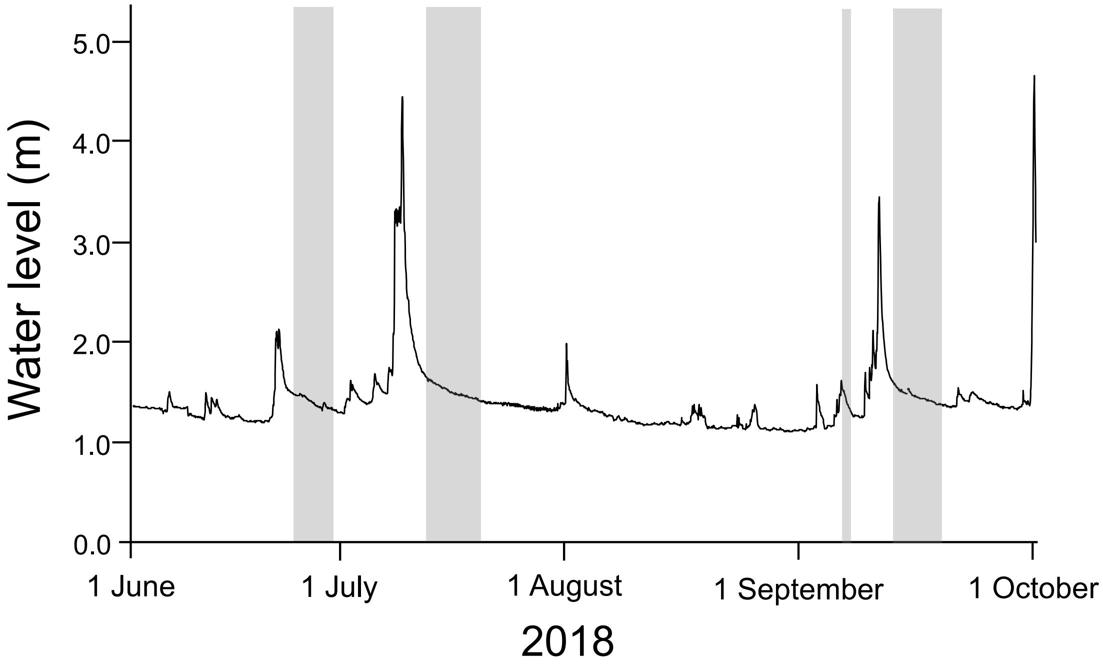

Fig. 2-1.2. Temporal changes in water level during the period from 1 June to 1 October 2018 at the Deai gauging station near the study area (Ministry of Land, Infrastructure, Transport and Tourism). The periods of the channel-selection survey are indicated by the shaded areas.

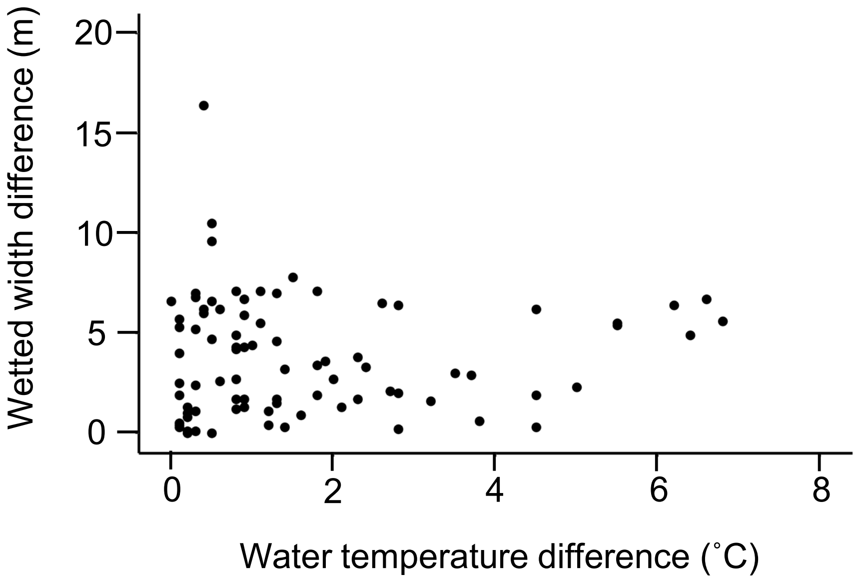

Fig. 2-1.3. Differences in wetted width and water temperature between pairs of the study channels for the channel-selection survey.

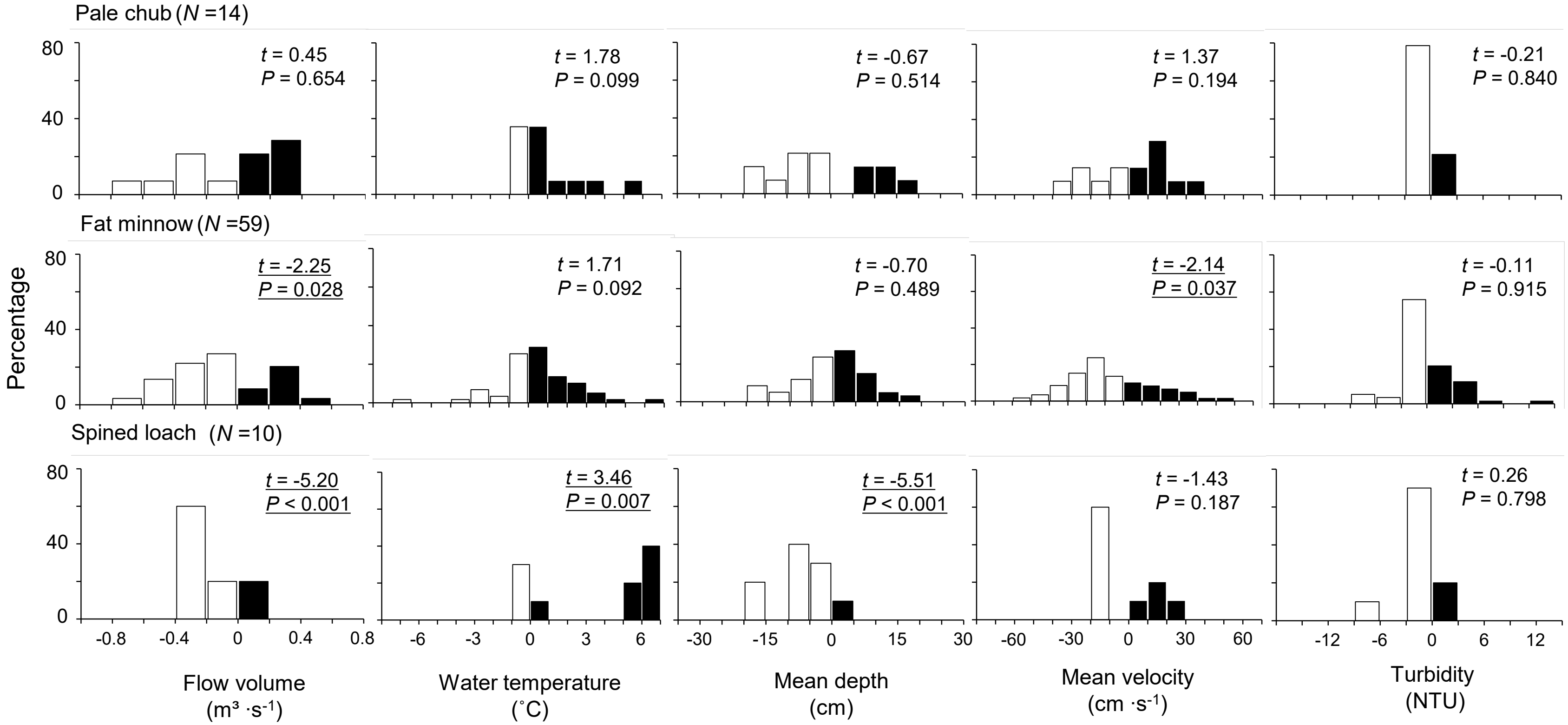

Fig. 2-1.4. Frequency distribution of differences in each variable between pairs of the study channel for the channel-selection survey. The values are produced by subtracting the value of "unselected" channel from that of "selected"; positive (solid) and negative (open) values indicate positive and negative responses, respectively.

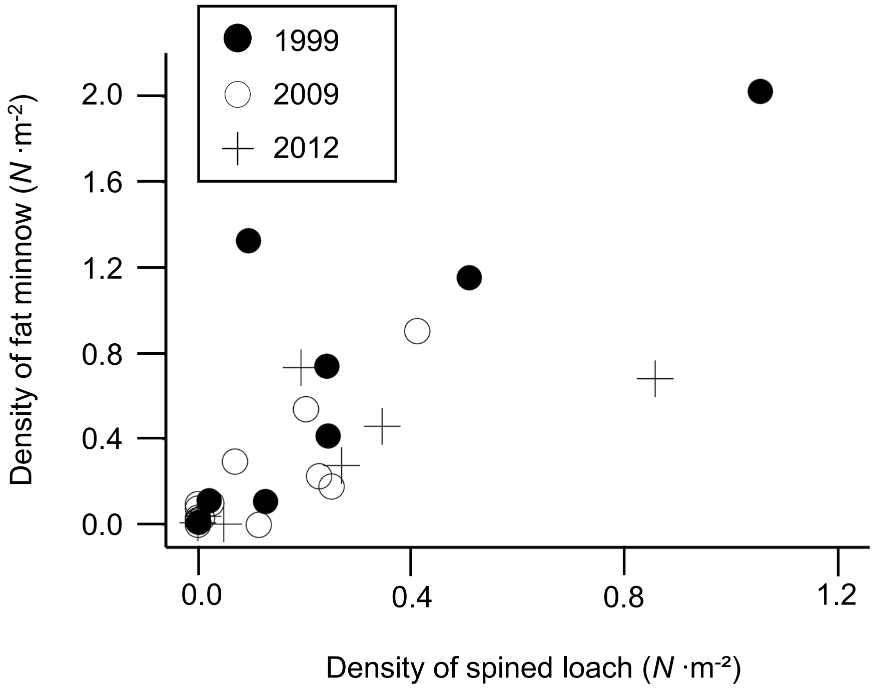

Fig. 2-1.5 Relationships between local density of fat minnow and that of spined loach in the braided channel network in three different years.

Table S2-1.1. Fish species captured by fyke nets in the channel-selection survey, listed in descending order of the number of individuals captured

Species	Number of individuals
Rhynchocypris oxycephala (fat minnow)	2984
Opsariichthys platypus (pale chub)	1074
Cobitis sp. BIWAE type A (spined loach)	623
Rhinogobius nagoyae (freshwater goby)	304
Candidia temminckii	109
Rhinogobius flumineus	76
Pseudogobio esocinus	36
**Rhinogobius* sp. OR	28
Silurus asotus	24
Tridentiger brevispinis	16
**Micropterus salmoides*	10
Plecoglossus altivelis	9
**Gymnogobius petschiliensis*	8
Anguilla japonica	7
**Lepomis macrochirus*	6
**Rhinogobius fluviatilis*	5
Cobitis shikokuensis	4
**Pseudorasbora parva*	3
**Carassius* sp.	2
**Gnathopogon elongatus*	2
**Cyprinus carpio*	2
Odontobutis obscura	2
**Tanakia limbata*	1
**Rhodeus ocellatus*	1
Total	5336

Asterisks indicate occasional species temporally immigrated from other habitats

Table S2-1.2. Means and SDs of environmental variables for selected and unselected channels by pale chub, fat minnow, and spined loach.

		Environmental variables				
		Flow volume ($m^3 \cdot s^{-1}$)	Water temperature (°C)	Mean depth (cm)	Mean velocity ($cm \cdot s^{-1}$)	Turbidity (NTU)
Pale chub	Selected	0.51±0.43	23.7±1.7	15.2±8.2	41.0±12.4	0.9±1.3
	Unselected	0.49±0.41	22.8±1.9	17.3±8.9	39.3±14.3	1.3±2.2
Fat minnow	Selected	0.32±0.34	21.9±2.0	14.5±7.4	28.7±16.1	2.5±3.3
	Unselected	0.40±0.27	21.4±2.3	15.5±6.8	35.1±19.2	2.4±3.1
Spined loach	Selected	0.11±0.17	25.3±2.0	9.4±1.8	20.6±17.1	0.7±1.5
	Unselected	0.31±0.14	21.7±1.8	17.2±6.7	21.8± 6.6	1.1±3.6

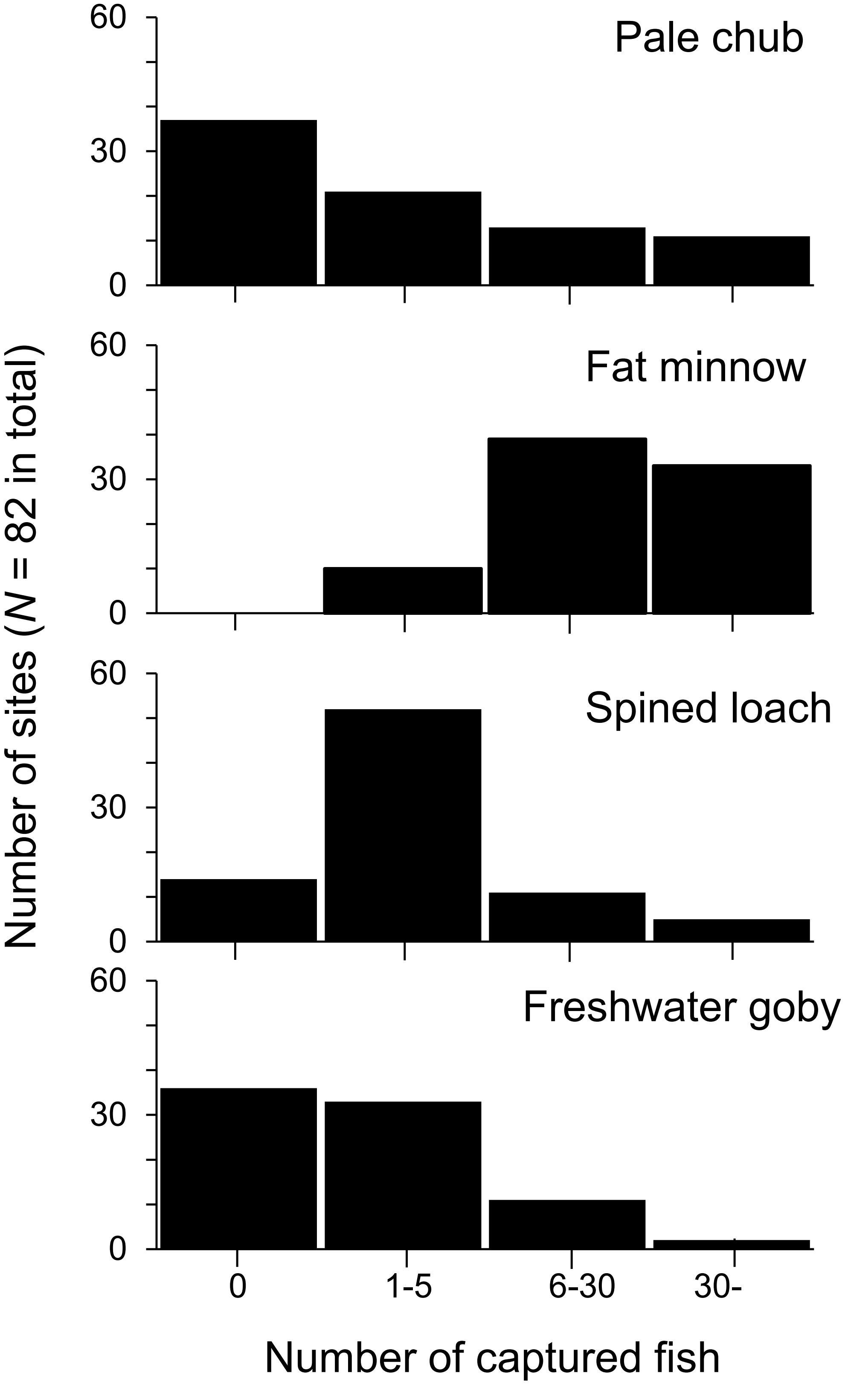

Fig. S2-1.1. Frequency histograms of the number of individuals captured by the two paired traps at each site (confluence).

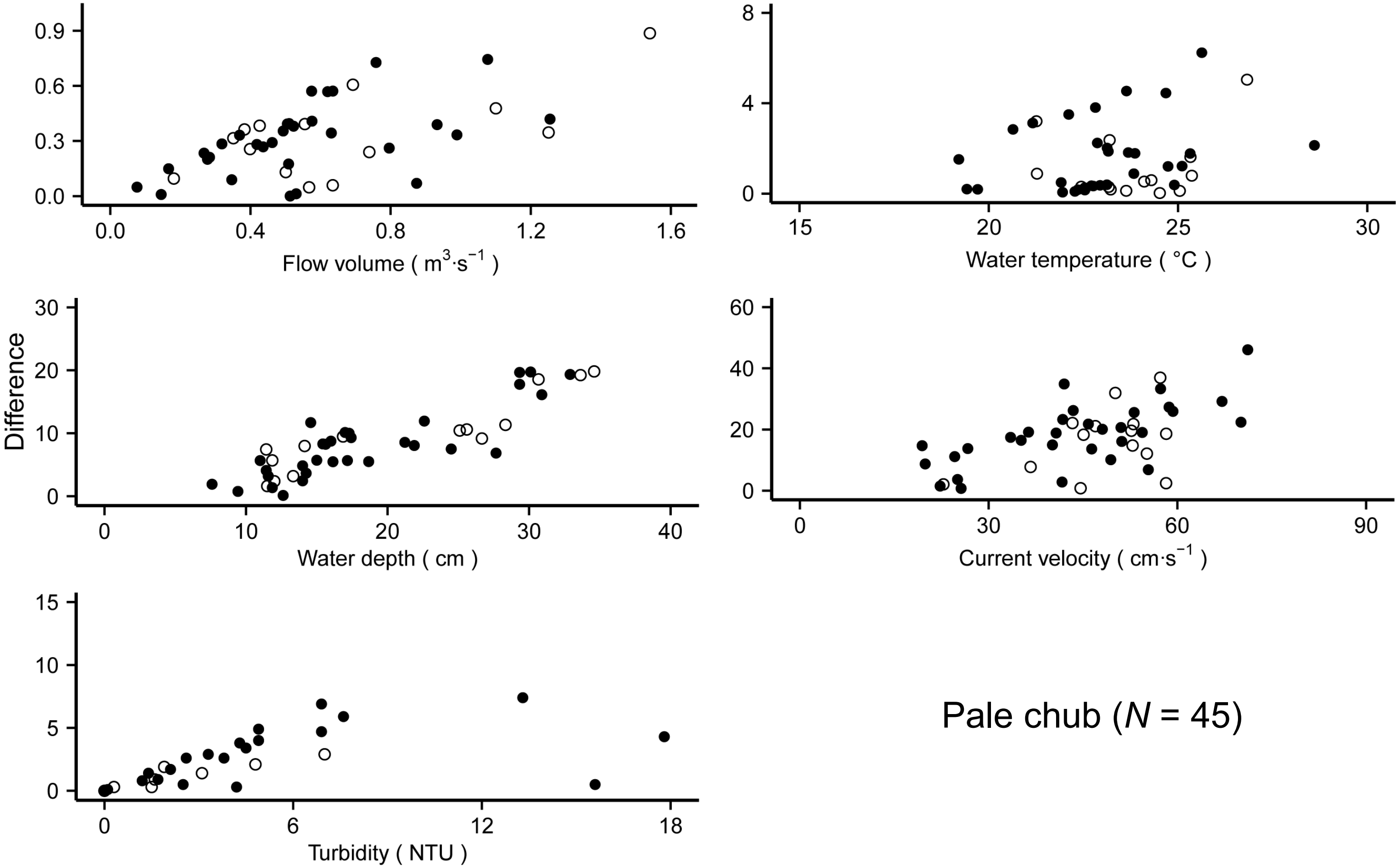

Fig. S2-1.2-1. Plots of differences in each environmental variable at confluences where pale chub was captured. Lateral axes represent the higher value of the paired channels at each confluence, with vertical axes representing the difference between the two paired values (higher minus lower). Open circles indicate confluences where the number of pale chub captured significantly differed between the two paired channels (binomial test), while solid circles indicate the other confluences.

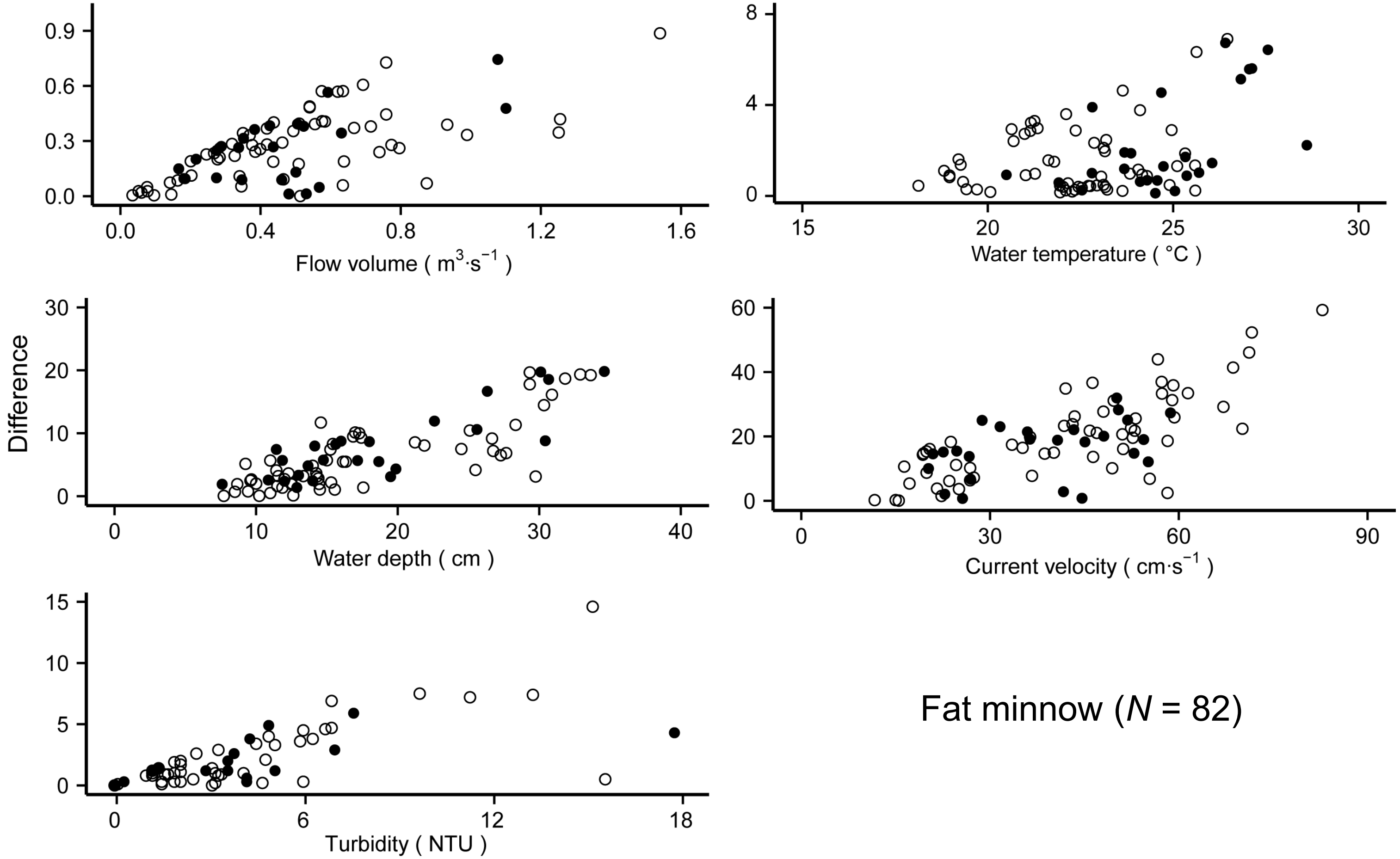

Fig. S2-1.2-2. Plots of differences in each environmental variable at confluences where fat minnow was captured. Lateral axes represent the higher value of the paired channels at each confluence, with vertical axes representing the difference between the two paired values (higher minus lower). Open circles indicate confluences where the number of fat minnow captured significantly differed between the two paired channels (binomial test), while solid circles indicate the other confluences.

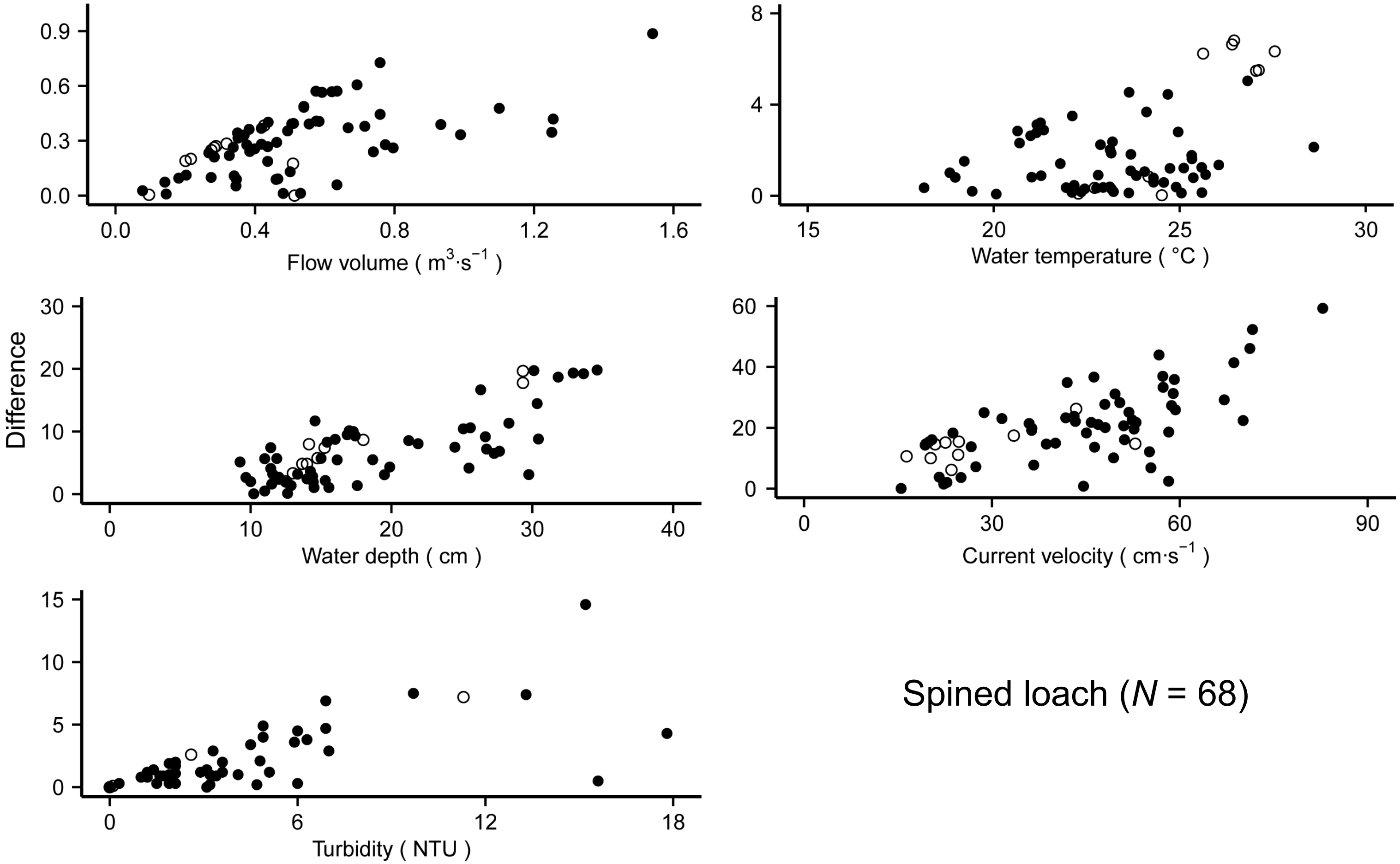

Fig. S2-1.2-3. Plots of differences in each environmental variable at confluences where spined loach was captured. Lateral axes represent the higher value of the paired channels at each confluence, with vertical axes representing the difference between the two paired values (higher minus lower). Open circles indicate confluences where the number of spined loach captured significantly differed between the two paired channels (binomial test), while solid circles indicate the other confluences.

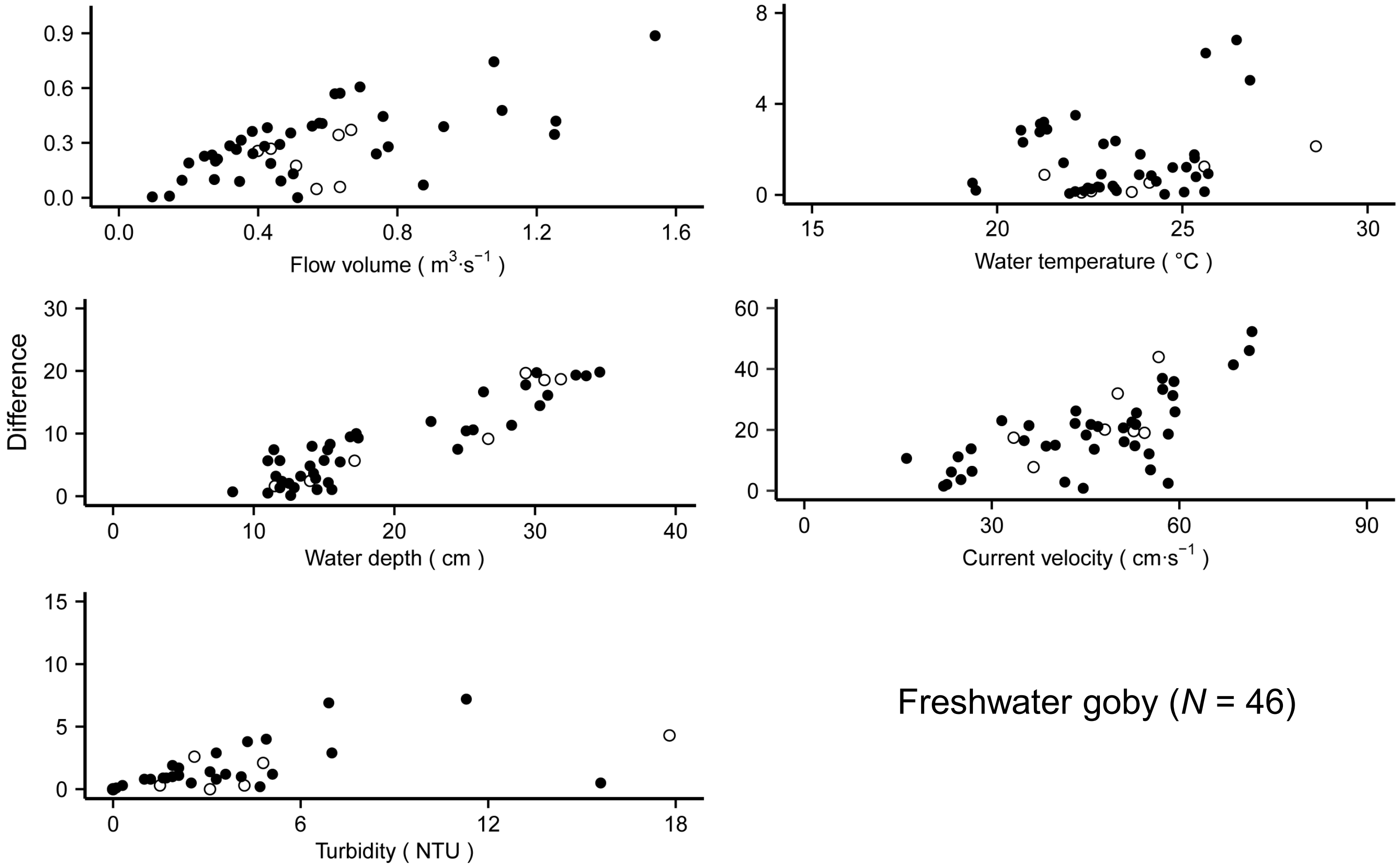

Fig. S2-1.2-4. Plots of differences in each environmental variable at confluences where freshwater goby was captured. Lateral axes represent the higher value of the paired channels at each confluence, with vertical axes representing the difference between the two paired values (higher minus lower). Open circles indicate confluences where the number of freshwater goby captured significantly differed between the two paired channels (binomial test), while solid circles indicate the other confluences.

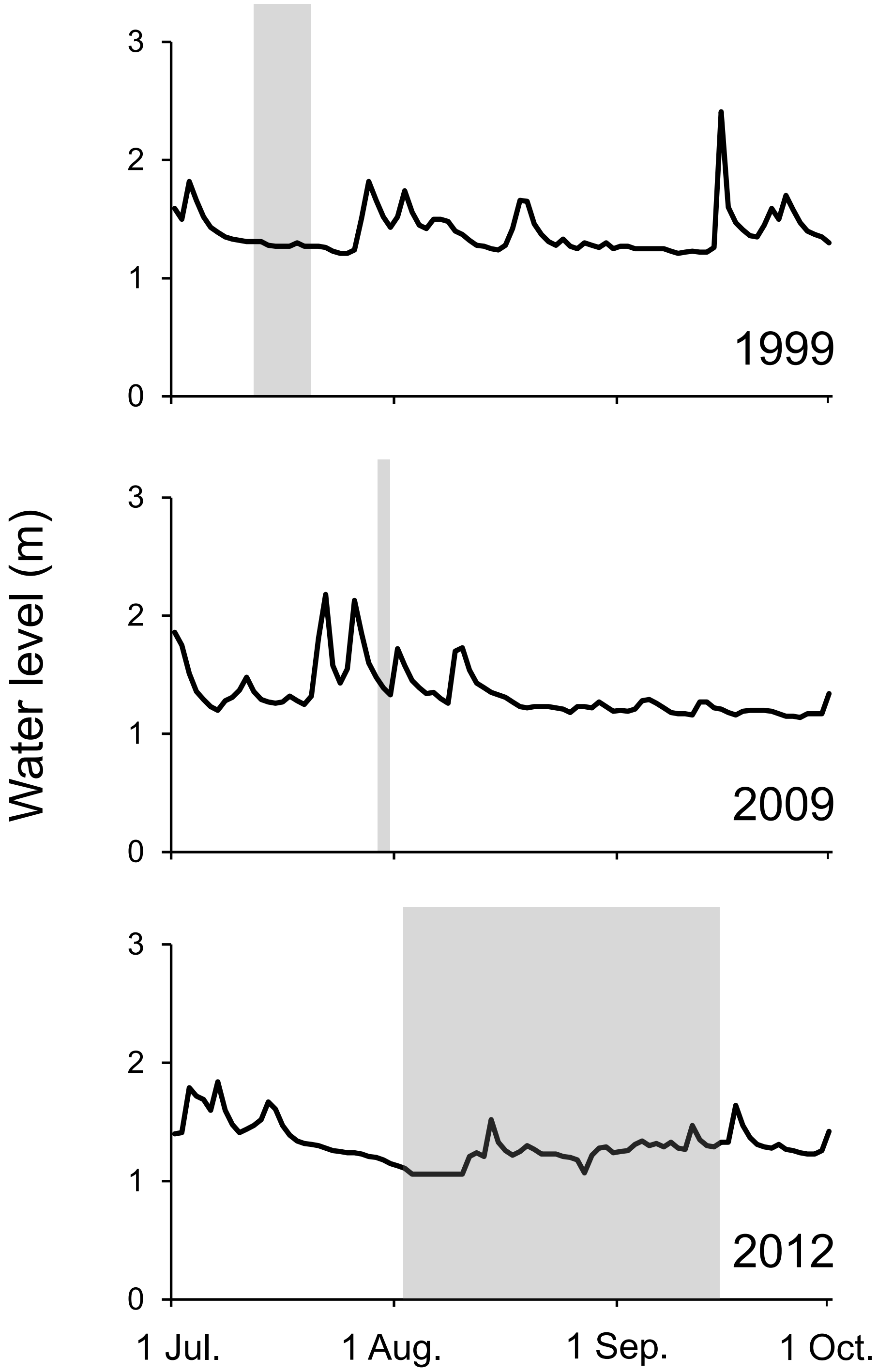

Fig. S2-1.3. Temporal changes in water level at the Deai gauging station near the study area (Ministry of Land, Infrastructure, Transport and Tourism) during the summer of 1999, 2009 and 2012. The periods of the fish survey are indicated by the shaded areas.

2-2. Seasonal habitat use by warmwater fishes in a braided river, southwestern Japan: effects of spatiotemporal thermal heterogeneity

2-2-1. Introduction

Spatiotemporal heterogeneity in environmental conditions is a fundamental driver of animal distribution and movement (Nathan et al. 2008). Rivers have complex networks of various habitats connected by water courses with each other (Ishiyama et al. 2016). Optimal habitats for fishes are generally distributed in patches across such networks and their distribution can change by season (Cooke et al. 2016). Therefore, fishes can benefit by moving among different habitats to exploit favorable conditions, and patterns of environmental heterogeneity in space and time within a system can affect persistence of populations inhabiting the system (Schlosser 1991; Northcote 1997; Brennan et al. 2019)

Water temperature is an important factor limiting the distribution and abundance of fishes, directly through their physiological tolerances and indirectly through temperature-dependent biotic interactions (Magnuson et al. 1979, Fausch et al. 1994; Taniguchi and Nakano 2000). River systems exhibit thermal gradients or heterogeneity at various spatial scales (Clark et al. 1999; Fullerton et al. 2015). The most common pattern is a downstream increase in water temperature at the watershed scale (Caissie 2006). Some species may exploit this longitudinal thermal gradient. For example, downstream movements for overwintering in response to decreasing water temperatures have been reported for cutthroat trout (*Oncorhynchus clarki*) and bull trout (*Salvelinus confluentus*) (Jakober et al. 1998; Brown 1999 and references therein). Although the longitudinal thermal gradient is common, it usually spans relatively long distances (kilometers: e.g. Torgersen et al. 1999; Fullerton et al. 2015), and movements over longer distances may involve higher costs and higher risks for fishes. Therefore, smaller-scale thermal heterogeneity, such as within-reach scale, may be more often exploited by fishes (Sullivan et al. 2021).

In summer, groundwater seeps or inflow from spring-fed tributaries can create localized areas of colder water in warm streams. Such coldwater patches can function as summer thermal refuge for coldwater fishes (Power et al. 1999; Sullivan et al. 2021). For example, Ebersole et al. (2001) found that rainbow trout (*Oncorhynchus mykiss*) used coldwater patches (3-8 °C colder than ambient temperature) created by groundwater seeps in warm streams (>22 °C) in summer. They subsequently showed positive effects of coldwater-patch frequency on salmonid abundance by conducting a more extensive survey (Ebersole et al. 2003). Similar use of coldwater patches that allow fish populations to persist during summer (heat stress) has often been reported (e.g. Matthews and Berg 1997; Brewitt and Danner 2014; Wang et al. 2020). Therefore, the role of small-scale thermal heterogeneity in creating coldwater refuges for fishes has now been well recognized. However, relatively few studies have examined warmwater patches in winter (Sullivan et al. 2021 for a review; but see Cunjak and Power 1986). Furthermore, although most studies on thermal refuges have focused on stenothermal, coldwater fishes, such as salmonids, less is known about warmwater species (but see Peterson and Rabeni 1996).

Braided rivers consist of networks of multiple channels with various environmental conditions (van der Nat et al. 2003; Gray and Harding 2009). As braided channels typically develop on thick alluvial deposits (e.g. alluvial fan), extensive ground- and surface-water interactions occur over braided reaches (Poole et al. 2002; Rodgers et al. 2004). Surface water sinks into the alluvium, whereas groundwater (or hyporheic water) emerges. As a result, distinct thermal heterogeneity is created within spatially limited areas (e.g. Arscott et al. 2001). Water temperature of groundwater-fed channels is cooler than that of surface-water-dominated channels in summer, and *vice versa* in winter. Close proximity of such channels having contrasting thermal regimes in braided reaches may play important roles in seasonal habitat use by fishes. Owing to their dynamic nature and highly heterogeneous environments, braided rivers have attracted considerable attention from hydrologists, geomorphologists and ecologists. Their various aspects, such as hydrological dynamics, thermal conditions, and community structure, have been reported (van der Nat et al. 2003; Rodgers et al. 2004; Arscott et al. 2005; Malard et al. 2006; Gray and Harding 2009). In particular, ecological studies have often emphasized important roles of habitat-type diversity unique to braided reaches in the maintenance of biodiversity, using benthic invertebrates (Burgherr et al. 2002; Arscott et al. 2005; Gray and Harding 2009). However, although spatio-temporal thermal heterogeneity in braided channels is well recognized (Arscott et al. 2001), its ecological functions for fishes have been less studied.

In this study, I described seasonal patterns of habitat use by two warmwater fishes, pale chub and freshwater goby, in a braided river. I analysed relationships between local fish densities and water temperature and other physical variables (e.g. water depth, current velocity) within two connecting channels having contrasting thermal regimes (groundwater-fed vs. surface-water-dominated channels), to examine whether fishes exploit the spatio-temporal thermal heterogeneity. In general, habitat use by stream fishes (expressed as position of individuals or point-abundance within stream reaches) is related to water depth and current velocity (e.g. Grossman and Ratajczak 1998; Peterson and Kitano 2019 for pale chub; Sone et al. 2001 for freshwater goby). If spatial thermal heterogeneity created by groundwater seeps affects habitat use by the two species, I predict that their local densities would be related to water temperature as well as water depth and current velocity.

2-2-2 Materials and methods

Study area

This study was conducted in the Shigenobu River (watershed area: 445 km^2; main stem length: 36 km) on Shikoku Island, Japan (Fig. 2-2.1). The climate of this region is warm-temperate, with mean monthly air temperature ranging from 6 to 28°C. The watershed receives an annual precipitation of ca. 1300 mm, with a rainy season spanning early summer to fall. This river has formed a large alluvial fan, owing to high sediment yield in its upper reaches. On the alluvial fan, the channel is braided and consists of groundwater (hyporheic) -fed and surface-water dominated streams, with the flow tending to be intermittent (Kawanishi et al. 2013). I selected two typical groundwater-fed and surface-water-dominated channels, which joined together (Fig. 2-2.1). These channels were selected because of their highest flow permanence (channels expected not to dry up throughout the study) among the unstable, braided channels in this intermittent segment. Habitat use by fishes was surveyed bimonthly from February to December 2019 within 500-m and 300-m reaches of the groundwater-fed and surface-water-dominated channels upstream from the confluence, respectively (hereafter, groundwater reach, surface-water reach). Channel size of the surface-water reach (wetted width at low flow: 8-20 m) was larger than that of the groundwater reach (5-10 m). Both reaches consisted of pools and riffles, with streambeds being dominated by pebbles and cobbles.

For the fish and habitat survey in each survey month, 1-m × 2-m quadrats were established at roughly 15-20-m intervals along the reaches, with their lateral locations being haphazardly determined, to cover habitat heterogeneity within the reaches. As a result, 27-30 and 22-23 quadrats were established in groundwater and surface-water reaches, respectively, from February to October (see Table S2-2.1). However, after the October survey, an upper part of the groundwater reach was disturbed by a civil engineering work. Therefore, this part was avoided in the December survey, and the number of quadrats was 19 and 22 in groundwater and surface-water reaches, respectively. In each quadrat, fish density and habitat variables were quantified. Water depth and current velocity at the quadrats ranged from 4 to 71 cm (mean: 20-30 cm) and from 0 to 167 cm·s^{-1} (mean: 20-40 cm·s^{-1}), respectively (Fig. 2-2.2)

Fish and habitat surveys

On each survey occasion, fishes in each quadrat were captured with single-pass electrofishing (Model 12 Backpack Electrofisher, Smith-Root Inc.). Captured fish with total length larger than 3 cm (including age-0 fish) were identified, counted and released. This fish survey was completed within one day. Fish abundance at each quadrat was expressed as density (the number of captured fish per m^2). It was difficult to use block nets without disturbing fishes, as the quadrat size was small. Therefore, I did not use block nets, and thus the fish density values should have been underestimated. However, the values can represent among-location differences in local fish abundance within the reaches, because all quadrats were surveyed in the same manner. A similar electrofishing procedure (point-abundance sampling without block net) has been frequently used as an effective method in habitat-use studies (e.g. Copp and Peňáz 1988; Mäki-Petäys et al. 1997; Kaspersson et al. 2012)

Water temperature, water depth, current velocity, and the presence/absence of cover were measured and recorded to characterize environmental conditions of each quadrat. Water depth (cm) was measured at three points (the center and upstream and downstream ends) of each quadrat. Current velocity (cm·s^{-1}) was also measured at the surface of the three depth-measurement points using a portable current meter (CKK-VR301, KENEK).Water depth and current velocity of each quadrat were represented by the mean of the three values. The presence or absence of cover within each quadrat was recorded. Instream large wood, concrete structure, aquatic macrophytes, and overhanging terrestrial vegetation (instream or within 40 cm of the water surface) were considered cover materials. These habitat surveys were conducted after the fish survey.

Water temperature at each quadrat was measured with a digital, electronic thermometer (TT-508, TANITA) once before the fish survey (around dawn). In the braided-channel network of the study area, I previously monitored water temperature at 10-min intervals using a data logger (HOBO Temp, Onset) at various locations for another purpose (Chapter 2-1), and then obtained 10 data sets of diel changes from different channels. Those monitoring data indicated that the lowest temperature was recorded around dawn, and water temperature recorded at dawn was strongly correlated with mean daily water temperature (r = 0.95, $P < 0.001$, $N = 10$). Therefore, water temperatures by snapshot measurements around dawn in this study broadly correspond to the daily minimum water temperature, but can represent among-location differences in daytime water temperature.

During the study period, water temperature in each quadrat ranged from 12.7 to 24.1 °C and 9.2 to 25.6 °C in groundwater and surface-water reaches, respectively (Fig. 2-2.2). Water temperature was higher in the groundwater reach than in the surface-water reach in winter (February and December), and the pattern was reversed in summer (from April to October). My study reaches are located in an intermittent segment of this river, and fishes are frequently affected by drying disturbances (Uchida and Inoue 2010; Kawanishi et al. 2013). In the study period, the most notable decline of water level occurred after the fish and habitat survey of June. In this phase, flow volume was exceedingly low in the braided channels, with some channels being fragmented into isolated pools. Furthermore, drying channels attract wading birds. In fact, during my bird monitoring (R. Morita and D. Togaki, unpublished), I often observed foraging flocks of egrets (*Ardea* spp.) around my study reaches during the low-flow period. Therefore, although neither of my two study channels dried up, effects of the low flow event through habitat contraction and bird predation on fishes potentially could have been ecologically significant.

Study species in the study system

Although a total of 21 species were captured during the study, the two species, pale chub and freshwater goby, comprised more than 90% in the total number of captured fish (Table S2-2.1). Therefore, these two species were examined in this study. Both species are typical warmwater species, being widespread and common in mid to lower reaches of rivers in the central and western Japan (Fujita 2015b; Hosoya 2015). Pale chub is a water-column fish, feeding on algae and invertebrates (Katano et al. 2006), while freshwater goby, which feeds mainly on invertebrates (Sone et al, 2001), is a typical benthic fish. The breeding season of both species is early summer (May to August: Nagoshi et al. 1962; Ito and Yanagisawa 2003), and their abundances generally increase from summer toward winter, owing to the recruitment of young-of-the-year. Freshwater goby is an amphidromous fish. Their hatched larvae descend to the sea, and return to rivers a few months after hatching (i.e. summer) as small age-0 juveniles (Sumizaki et al. 2019; M. Shibuya, unpublished). Although pale chub is not diadromous, this species is highly mobile. Long-distant movement of pale chub has been suggested by a study conducted in the study area (Uchida and Inoue 2010). My braided channels of the Shigenobu River are a highly dynamic system, with multiple channels becoming connected, disconnected, and sometimes dry up, depending on changes in the water level. At high-flow events, fish movement over the channel network is facilitated, and dried channels are rapidly recolonized. That is, fishes are continuously redistributed over the network (see Uchida and Inoue 2010). As the study area is such a dynamic system, I can assume that both species individuals can frequently move between the two connecting study reaches and respond to local habitat conditions within the reaches.

Statistical analysis

To evaluate differences in the density of each species between the two study reaches and among survey months, I performed two-way analysis of variance (ANOVA), using reach and month as main factors. Relationships between fish densities and habitat variables at the quadrats were examined by generalized linear models (GLM), using the package "MuMIn" in R v.4.0.3 (R Core Team 2020). I constructed GLMs with a gaussian error distribution, with $\log_{10}$-transformed density of each species as a response variable. Logarithmic transformation of the response variables was conducted to improve normality. Explanatory variables were water temperature, water depth, current velocity and the presence/absence of cover. The values of each numerical explanatory variable were transformed to z-scores (mean = 0 and SD = 1) to standardize the variation among the three variables (temperature, depth, and velocity). I constructed all possible models with different sets of explanatory variables, and the model performance was evaluated using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). The model with the lowest AICc value and the models with ΔAICc (AICc difference from the best model) < 2 were considered the best and equivalent models, respectively. On the basis of these best and equivalent models, I performed model averaging and calculated the relative variable importance (RVI) using Akaike weights (Burnham & Anderson, 2002) to assess the relative importance of the explanatory variables. This analysis was conducted separately by month, because I assumed that the relationships between fish density and habitat variables changed with season.

2-2-3. Results

Seasonal changes in the densities of the two species were similar in that 1) the densities in the surface-water reach once peaked in June, 2) the densities in both reaches were lowest in August, and 3) increased toward winter (October, December) (Fig. 2-2.3). Two-way ANOVA showed significant reach × month-interaction effects on both densities (Fig. 2-2.3), indicating that between-reach differences in their densities changed with season. Pale chub density was higher in the groundwater reach than in the surface-water reach in February, and it was reversed from April to August, and returned from October. Freshwater goby density exhibited a similar pattern. In February, the goby density was also higher in the groundwater reach than in the surface-water reach. The density in the surface-water reach subsequently increased toward summer, while that in the groundwater reach decreased. During the increasing phase from August toward winter, the groundwater reach had higher density than the surface-water reach.

Model selection and RVI for pale chub indicated that local density of pale chub was related to the four variables, water temperature, water depth, current velocity and cover, with their relative importance changing by month (Table 2-2.1). In February and April, positive effects of water temperature had the highest RVI values followed by cover. Water depth also had the highest value in April, and it was maintained in June. In June and August, positive effects of current velocity had the highest RVI values. In October and December, RVI values of water temperature and cover were higher than or the same as that of water depth, although effects of cover were positive in October while negative in December. In summary, water temperature had positive effects throughout the year, except June (Table 2-2.1, Fig. 2-2.4). Water depth often had positive effects, whereas positive effects of current velocity was limited to summer. RVI of cover was high in some months, but its effects were inconsistent.

Model selection and RVI for freshwater goby indicated that current velocity positively affected the goby density throughout the year, with the highest RVI values in all months (Table 2-2.2). Water temperature also exhibited the highest RVI values in February, April, October and December, but its effects were inconsistent, being positive in February and December whereas negative in April and October (Fig. 2-2.4). Although cover had negative effects throughout the year, its RVI values were lower than those of current velocity and water temperature (except December).

2-2-4. Discussion

In the study river, although some similarities were found between the two reaches in the temporal changes of the two species' densities, contrasting between-reach differences were also found. The analysis using GLMs showed that spatial variation of each species' densities within the two reaches were related to water temperature, as well as water depth and current velocity in most of the months. In particular, consistent effects of water temperature were detected for pale chub, suggesting that the seasonal patterns of pale chub density across the two reaches were affected by the spatio-temporal variation of water temperature. These results suggest that spatio-temporal thermal heterogeneity created by the two contrasting channels played a role in habitat use by fish.

In the temporal changes of the fish densities, declines in August and subsequent increases toward winter were common between the two species and the two reaches. The common decline in August was probably caused by the low-flow event occurred after the survey in June. In general, habitat contraction (decrease of water volume) increases fish mortality through extremes of abiotic conditions (e.g. high temperature, low dissolved oxygen) and intensified biotic interactions (predation and competition) (Magoulic and Kobza 2003). In my case, stranding and bird predation associated with the low-flow event likely decreased the number of individuals of both species in the two reaches, because many egrets foraging along drying channels were observed at the low-flow period. On the other hand, increases of the densities toward winter were due to recruitment of age-0 individuals. The breeding season of both species is early summer (May to August: Nagoshi et al. 1962; Ito and Yanagisawa 2003), and their newly emerged larvae grow to catchable size by winter. The seasonal pattern common between the two species and the two reaches was likely shaped by the low-flow event and recruitment.

Although such a common pattern was observed (i.e. decline of the densities in August and subsequent increase toward winter), patterns of temporal changes in fish densities differed between the groundwater and surface-water reaches, especially clearly in pale chub. From February to June, pale chub density in the groundwater reach declined, while that in the surface-water reach increased. These contrasting trends between the two adjacent reaches suggest movement of pale chub from the groundwater to the surface-water reach. In August, the trends from June were disrupted by the low-flow event. From October to December, although pale chub density in both reaches increased similarly, that was higher in the groundwater reach than in the surface-water reach. Overall, pale chub density was higher in the groundwater reach than in the surface-water reach in winter, and *vice versa* in summer. This pattern is similar to that in water temperature (Fig. 2-2.2), and the GLMs showed that spatial variation in pale chub density in each month was generally related to a positive effect of water temperature in combination with water depth and/or current velocity.

Pale chub is known as a typical warmwater species, being numerically dominant in mid- to lower reaches of rivers in the central and southwestern Japan (Hosoya 2015). Although this species is rather a habitat generalist, they generally use slow-current habitats such as pools in winter, and shift their use to faster current habitats (runs, riffles) toward summer (Nagoshi et al. 1962). GLMs showed that positive effects of current velocity on pale chub density became evident from April to August. This suggests that pale chub shifted their habitat use to faster currents toward summer, being consistent with the general seasonal trend. In April and August, water temperature also had positive effects independently of depth and velocity (Table 2-2.1), suggesting avoidance of colder water by pale chub. From April, water temperature in the groundwater reach became lower than that in surface-water reach, and below 20°C even in June (Fig. 2-2.4). Pale chub likely avoided such a colder, groundwater-fed stream during summer. I previously examined channel selection by fishes at confluences of the braided-channel network of this study area, and found that pale chub avoided channels with lower water temperature during post-spate movement in summer (Chapter 2-1). Summer water temperature of the groundwater reach may be suboptimal for pale chub in comparison with that in the surface-water reach. In contrast to April-August, the groundwater reach had higher pale chub density than the surface-water reach in winter (February and December), and the density was related to positive effects of water temperature in combination with depth (positive) or velocity (negative). Overall, these results suggest that thermal heterogeneity created by groundwater seeps affected habitat use by pale chub both in summer and winter.

Between-reach differences in seasonal changes of freshwater goby density were similar to those of pale chub in that 1) trends from February toward summer were contrasting and 2) the groundwater reach had higher density than the surface-water reach in winter. This similarity suggests effects of thermal heterogeneity similar to those on pale chub. However, important variables in explaining the goby density shown by GLMs were different from those for pale chub. Freshwater goby is also a typical warmwater species, and is well known to prefer habitats with fast currents and coarse substrates (Sone et al. 2001; Oto and Masuda 2019). GLMs showed that the density of freshwater goby was related to a positive effect of current velocity throughout the year, being consistent with the general knowledge. Although water temperature was also an important variable affecting the goby distribution as its RVI value and average coefficient were as high as those of current velocity, its effects varied by month. Unlike pale chub, the goby density was negatively affected by water temperature in April, August and October. This suggests that, in non-winter seasons, freshwater goby did not avoid colder water. On the other hand, the higher goby densities in the groundwater reach than in the surface-water reach in winter (February and December) were related to higher water temperature, suggesting that freshwater goby also preferred warmer water in winter.

For the two warmwater species, winter would be a harsh season. Nagoshi et al. (1962) mentioned that the activity of pale chub declines in winter, when water temperature is below 10 °C. Similarly, Sawara (1978), who examined seasonal changes in growth, stomach contents, and feeding activity of freshwater goby, showed a decline of their stomach fullness in winter and documented that the goby individuals became inactive, hiding under cobbles from the end of November, when water temperature was below 15 °C. Such a reduced behavioral performance in winter would lead to higher predation risks from homeothermic animals such as birds (Cunjak 1996; Hurst 2007). In addition, cold temperature in winter increases fish mortality through depletion of energy reserves and decline of physiological conditions (Sawara 1978; Cunjak 1996; Hurst 2007). Therefore, both pale chub and freshwater goby can benefit from the use of the warmer groundwater reach adjacent to the cold, surface-water reach by maintaining their activity and decreasing winter mortality. Such a function of warmwater areas as an overwintering habitat is generally known in salmonids in boreal regions (e.g. Cunjak 1996), where winter conditions are so severe that air temperature declines to far below 0 °C and streams are usually frozen. This study dealing with warmwater fishes revealed that, even in warm-temperate regions (e.g. winter minimum water temperature > 5 °C), groundwater seeps can play an important role in overwintering of fishes. A similar role of a spring stream has been shown for warmwater species, such as centrarchids (Peterson and Rabeni 1996).

Spatio-temporal environmental heterogeneity of braided channels and its effects on their biota have often been examined, especially in terms of the maintenance of biodiversity (e.g. Gray and Harding 2009). In Japan, braided channels are typically formed on alluvial fans, of which location is the transition between steep mountainous regions and gentle lowland plains (Oguchi et al. 2001). This location also often corresponds to the transition between coldwater- and warmwater-species zones of fish fauna. In such situations, which may be found in other temperate regions of the world, coexistence of coldwater and warmwater species can be facilitated in braided reaches through spatio-temporal heterogeneity of thermal conditions. In summer, warmwater species may avoid coldwater patches created by groundwater seeps, while such coldwater patches can function as critical thermal refuge for coldwater species (see Sullivan et al. 2021 for a review). In winter, groundwater seeps then create warmwater patches that can provide an overwintering habitat for warmwater species. Although my study examined only a pair of two connecting channels, my results suggest that the close proximity of channels having contrasting thermal regimes is an important aspect of braided rivers for persistence of diverse fish assemblages.

Table 2-2.1. Model selection results for pale chub

		Explanatory variable						
	Intercept	Temperature	Depth	Velocity	Cover	AICc	ΔAICc	Akaike's weight
February	1.38	0.74		-0.34	+	178.5	0.00	0.36
	1.38	0.83			+	179.6	1.09	0.21
	1.38	0.71		-0.44		180.1	1.65	0.16
Average	1.38	0.77		-0.37	+			
RVI		1.00	0.00	0.71	0.78			
April	-7.04	0.45	0.29			100.3	0.00	0.30
	-7.92	0.50	0.29		+	100.7	0.40	0.24
	-6.73	0.43	0.32	0.13	+	100.9	0.63	0.22
	-6.08	0.39	0.31	0.09		101.7	1.43	0.15
Average	-7.13	0.45	0.30	0.11	+			
RVI		1.00	1.00	0.41	0.51			
June	1.08		0.68	0.60		144.7	0.00	0.60
Average	1.08		0.68	0.60				
RVI		0.00	1.00	1.00	0.00			
August	-2.14	0.10		0.13		73.3	0.00	0.23
	0.18			0.10		74.6	1.32	0.12
	0.18					74.7	1.38	0.11
	-1.55	0.07				74.9	1.57	0.10
Average	-1.10	0.09		0.12				
RVI		0.59	0.00	0.63	0.00			
October	3.47				+	168.9	0.00	0.22
	-8.42	0.57			+	169.6	0.69	0.16
	-14.97	0.88				170.0	1.07	0.13
Average	-5.01	0.71			+			
RVI		0.57	0.00	0.00	0.75			
December	4.67	0.57	0.64		-	144.7	0.00	0.50
Average	4.67	0.57	0.64		-			
RVI		1.00	1.00	0.00	1.00			

Regression coefficients of the best and equivalent models (ΔAICc < 2) and relative variable importance (RVI) are shown.

Table 2-2.2. Model selection results for freshwater goby

		Explanatory variable						
	Intercept	Temperature	Depth	Velocity	Cover	AICc	ΔAICc	Akaike's weight
February	1.52	0.69		0.49	-	150.3	0.00	0.32
	1.52	0.66	-0.28	0.58		151.0	0.92	0.22
Average	1.52	0.68	-0.28	0.52	-			
RVI		1.00	0.64	1.00	0.75			
April	21.48	-1.16		0.33	-	114.3	0.00	0.41
	20.59	-1.11		0.39		115.3	0.97	0.25
	20.03	-1.08	-0.11	0.31	-	115.7	1.35	0.21
Average	20.50	-1.13	-0.11	0.33	-			
RVI		1.00	0.24	1.00	0.72			
June	1.96		0.24	0.59		136.6	0.00	0.36
	1.96			0.59		138.0	1.33	0.19
Average	1.96		0.24	0.59				
RVI		0.00	0.65	1.00	0.00			
August	4.56	-0.16		0.35		118.7	0.00	0.28
	5.02	-0.18	-0.12	0.36	-	119.5	0.85	0.19
	4.13	-0.14		0.33		120.0	1.34	0.15
	0.80			0.40		120.4	1.75	0.12
Average	3.96	-0.16	-0.12	0.36	-			
RVI		0.89	0.26	1.00	0.20			
October	23.57	-1.03		0.67	-	167.4	0.00	0.37
	28.95	-1.29		0.74		168.5	1.06	0.22
Average	25.59	-1.12		0.70	-			
RVI		1.00	0.00	1.00	0.63			
December	2.90	0.92		0.41	-	126.9	0.00	0.57
	2.87	0.87	-0.18	0.39	-	128.5	1.61	0.26
Average	2.89	0.90	-0.18	0.40	-			
RVI		1.00	0.40	1.00	1.00			

Regression coefficients of the best and equivalent models (ΔAICc < 2) and relative variable importance (RVI) are shown.

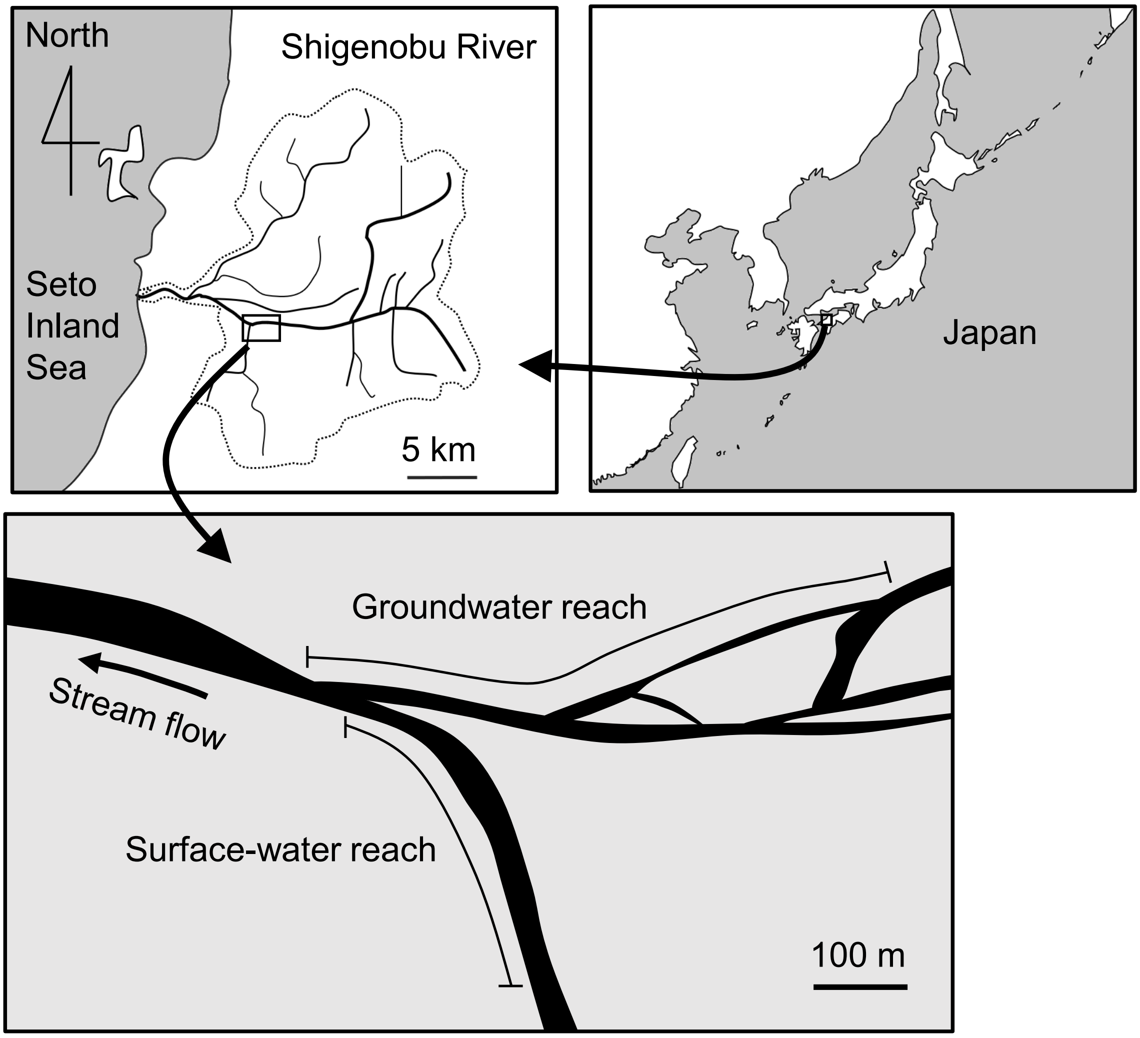

Fig. 2-2.1. Location (upper) and map (lower) of the study area in the Shigenobu River.

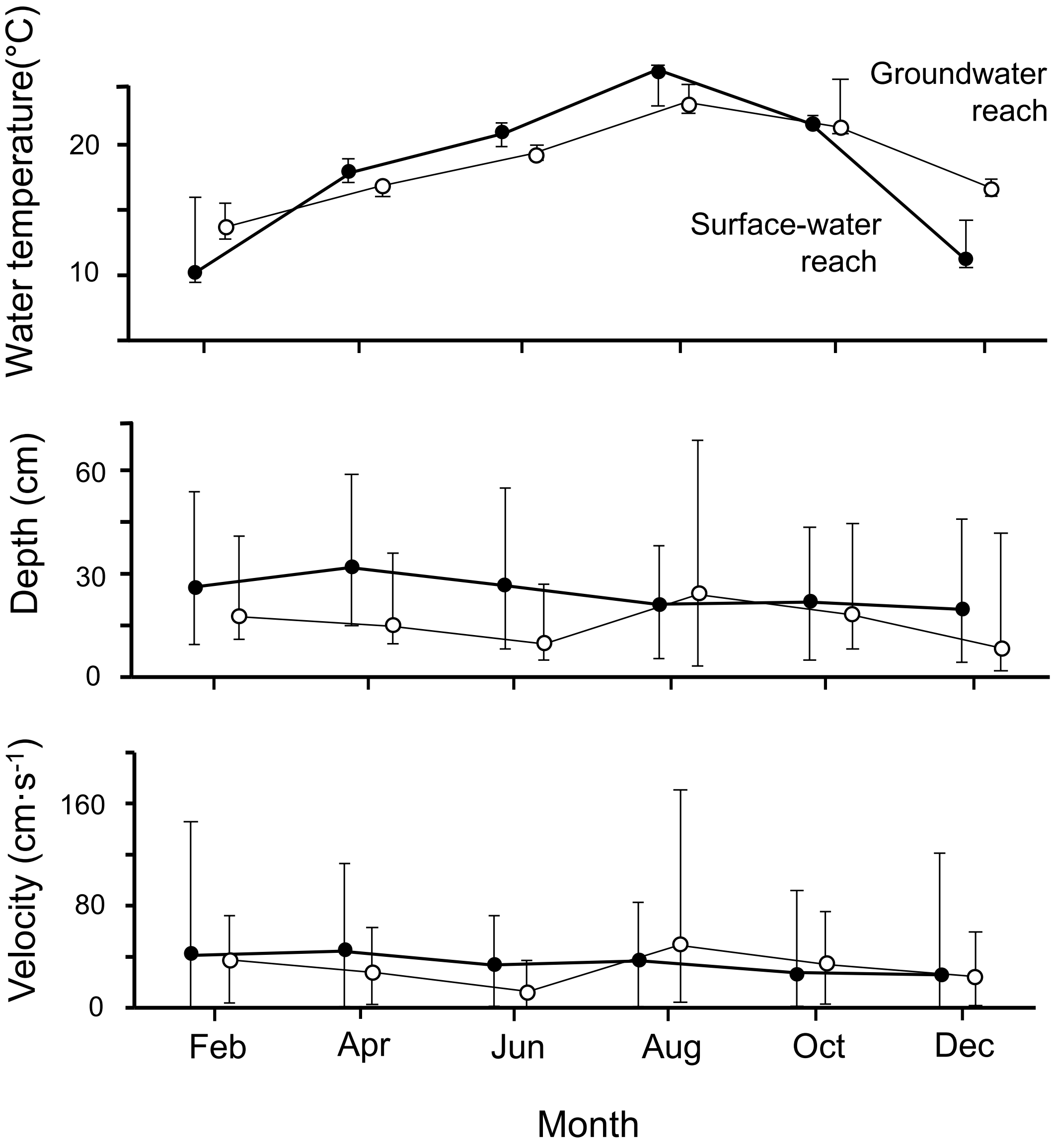

Fig. 2-2.2. Mean and range of water temperature, water depth, and current velocity at the quadrats in the groundwater (open circle) and surface-water (solid circle) reaches.

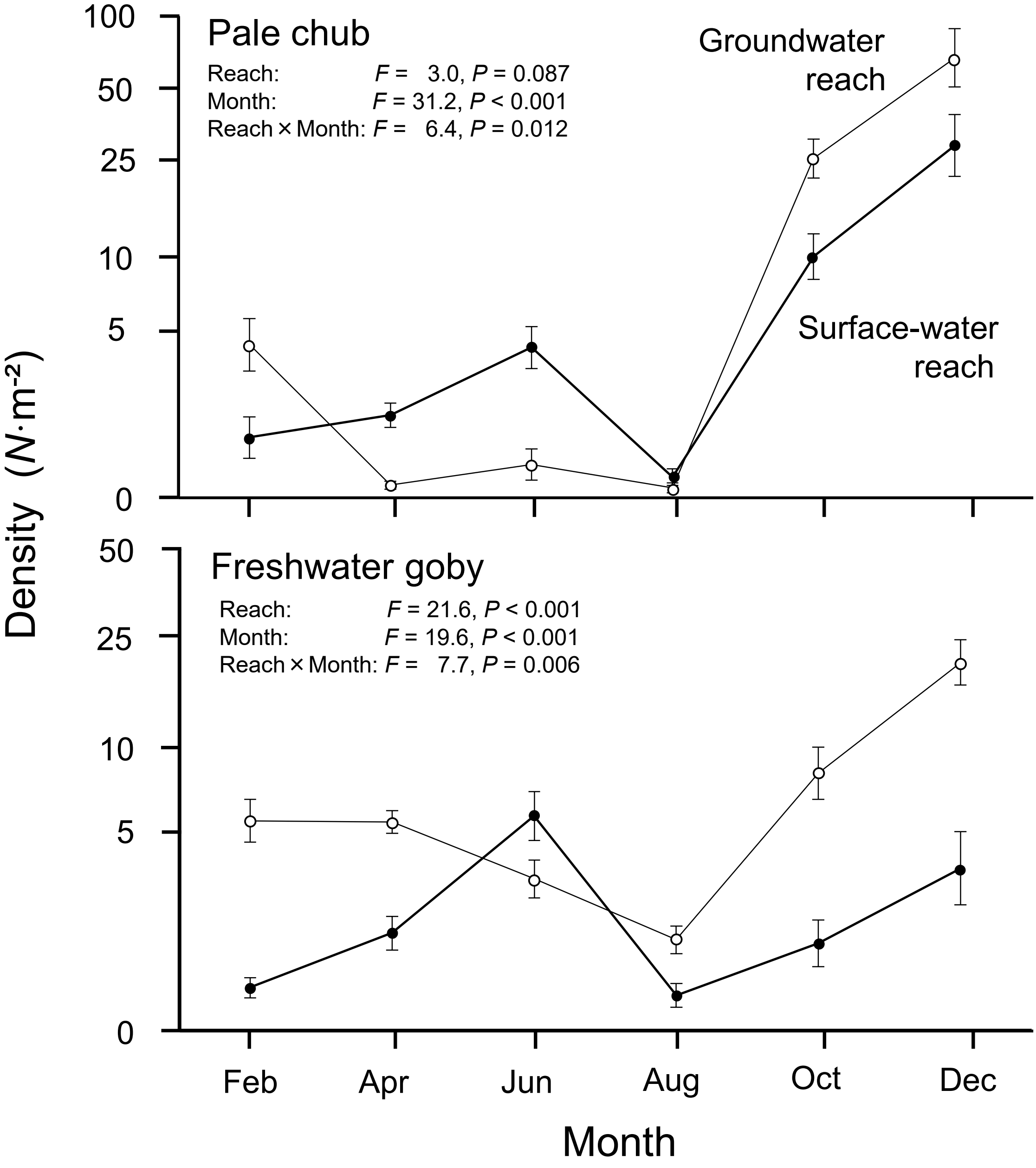

Fig. 2-2.3. Seasonal changes of the density of pale chub (upper) and freshwater goby (lower) in the groundwater (open circle) and surface-water (solid circle) reaches. The axis of fish density is on a logarithmic scale.

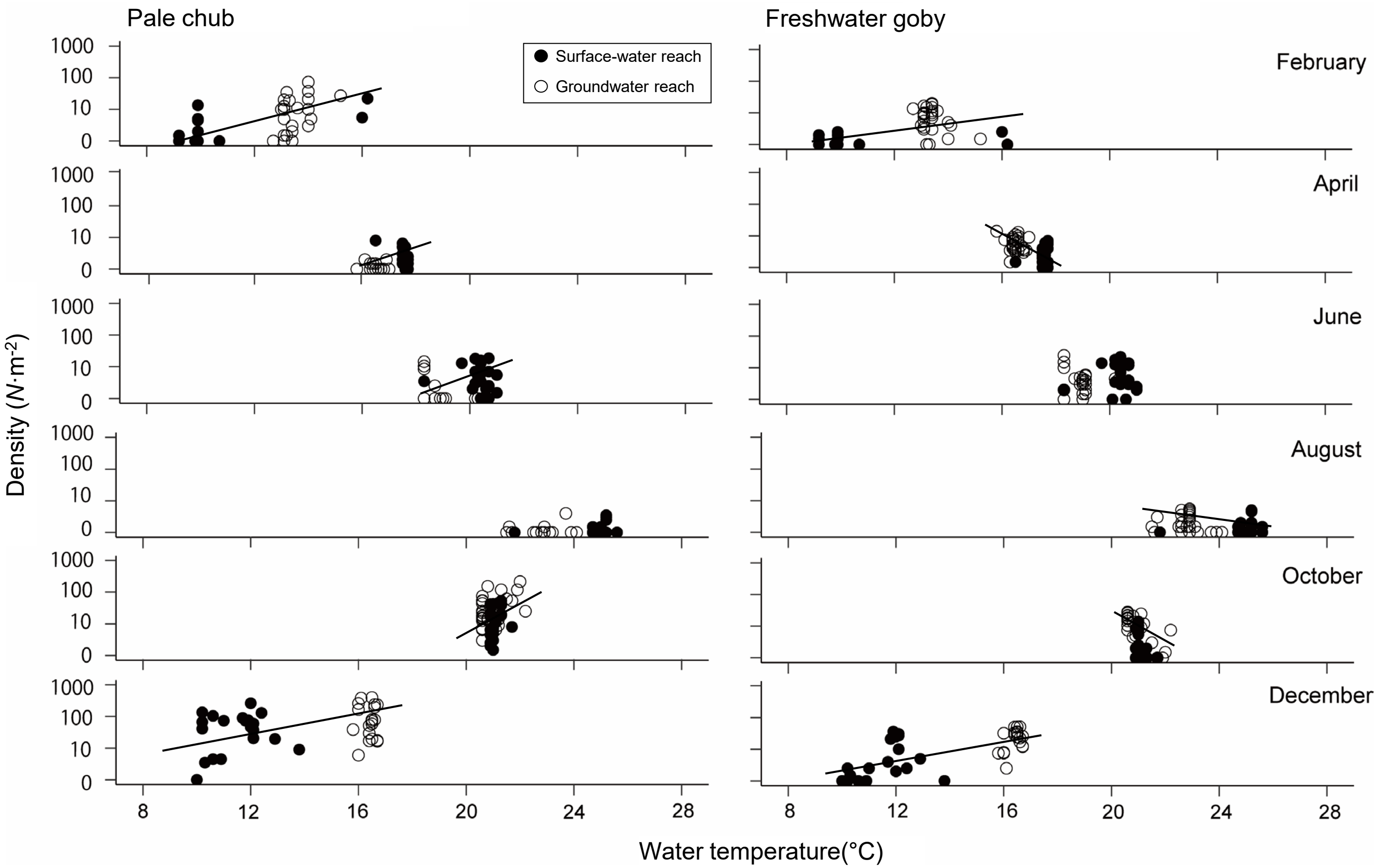

Fig. 2-2.4. Density of pale chub (left) and freshwater goby (right) in relation to water temperature in each month. Regression lines are drawn for significant correlations (Pearson's *r*, *P* <0.05). Open and solid circles represent values of groundwater and surface-water reaches, respectively. The axis of fish density is on a logarithmic scale.

Table S 2-2.1. Fish species captured in each survey month, listed in descending order of their abundance. *N* indicates number of quadrats in groundwater and surface-water reaches, respectively.

Species (*N*)	Feb (30,22)	Apr (30,23)	Jun (27,23)	Aug (30,23)	Oct (30,23)	Dec (19,22)	Total
Opsariichthys platypus (pale chub)	678	81	307	22	3216	7738	12042
Rhinogobius nagoyae (freshwater goby)	442	391	540	115	806	1711	4005
Cobitis sp. BIWAE type A	52	29	14	6	75	192	368
Rhynchocypris oxycephala	2	4	86	45	68	19	224
Tridentiger brevispinis	8	9	25	3	20	57	122
Cobitis shikokuensis	0	11	2	12	75	1	101
Pseudogobio esocinus	15	5	11	1	18	6	56
Candidia temminckii	4	18	3	0	4	5	32
Rhinogobius fluviatilis	2	2	2	0	17	8	31
Anguilla japonica	0	2	5	1	5	4	17
Rhinogobius flumineus	9	0	0	0	3	3	15
Silurus asotus	0	7	0	0	2	1	10
Carassius sp.	0	0	0	2	7	1	10
Cyprinus carpio	0	0	0	2	5	0	7
Lepomis macrochirus	0	0	0	1	4	1	6
Rhinogobius sp. OR	1	0	0	0	3	1	5
Pseudorasbora parva	0	0	0	1	2	0	3
Odontobutis obscura	0	0	0	0	1	2	3
Sicyopterus japonicus	0	0	1	0	0	0	1
Oryzias latipes	0	0	0	0	1	0	1
Gymnogobius petschiliensis	0	0	0	0	1	0	1
Total	1213	559	996	211	4333	9750	17060

2-3. Conclusion: importance of habitat connectivity

In this chapter, I examined 1) channel selection by fish and its effect on assemblage organisation, and 2) spatio-temporal variations in fish density at a confluence of two channels with contrasting thermal regime, using a braided river. The results showed that 1) channel selection by fish at confluences during their movement is a notable factor determining local fish assemblage and 2) such channel selection can change depending on season and fishes can benefit from seasonal movement between different habitats to exploit favorable conditions. The effects of channel selection on the assemblage organisation of pools shown in chapter 2-1 and seasonal and between-channel variations in fish densities shown by chapter 2-2 suggest prominent effects of regional processes in determining local fish assemblage and the importance of habitat connectivity in maintaining fish assemblage in the braided river.

The importance of habitat connectivity of the braided-channel network shown by this chapter may also be applied to larger aquatic networks of lowland rivers, such as river-floodplain systems. Similar to braided channels, aquatic systems of lowland rivers consist of various habitats with different environmental conditions including thermal heterogeneity, and fish frequently move across different habitats (Ishiyama et al. 2016; Steel et al. 2017; Stoffels et al. 2022). For example, deepbody bittering (*Acheilognathus longipinnis*) move into floodplain waterbodies for spawning during typhoon-fed flooding (Nagayama et al. 2022). In their study system, abundance of deepbody bittering in isolated waterbodies was less than that in connected waterbodies, suggesting that habitat connectivity would be important for maintenance of their population. In Japan, floodplain-river systems, such as networks of rivers, tributaries, ponds and paddy fields, have been degraded and fragmented by irrigation and land development during the last decades (Ishiyama et al. 2016). Such habitat degradation river-floodplain systems is one major factor of the loss of species diversity in river systems (Ishiyama et al. 2016; Schofield et al. 2018; Stoffels et al. 2022). In the Shigenobu River, slender bittering (*Tanakia lanceolata*) has been decreased rapidly for the two decades. This decrease may be due to degradation of floodplain habitats (e.g. agricultural ditches), because slender bittering uses unionid mussels in ditches associated with paddy fields as a spawning substrate (Uemura et al. 2018). In lowland river systems, fish would benefit from movement across various habitats with different environmental conditions, because optimal habitats for fish are distributed across river network and change depending on season and life stage (Cooke et al. 2016; Schofield et al. 2018). Therefore, my results from a braided river suggest that habitat heterogeneity and connectivity across networks of river-floodplain systems are important in maintaining fish assemblage in lowland river systems.

3. Interspecific interactions in headwater streams

Longitudinal species replacement has often been reported for various pairs of stream salmonids, such as Dolly Varden (*S. malma*) and white-spotted charr (*S. leucomaenis*) (Fausch et al. 1994), bull charr (*S. fontinalis*) and rainbow trout (*O. mykiss*) (Torgersen et al. 2006), cutthroat trout (*O. clarki*) and rainbow trout (Reeves et al. 2011), and white-spotted charr and masu salmon (*O. masou*) (Miyasaka et al. 2003). Condition-specific competition, in which competitive superiority changes along longitudinal environmental gradients, has been considered one major mechanism of such species replacement (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000).

Most previous studies on condition-specific competition regarding longitudinal replacement of salmonids have focused on interference competition for feeding habitat (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000; McMahon et al. 2007), probably because stream salmonids are famous for their territorial feeding behaviour in a dominance hierarchy (e.g. Fausch 1984; Nakano 1995a, b). For example, Taniguchi and Nakano (2000) successfully showed that negative effects of white-spotted charr on Dolly Varden through interference behaviour in feeding were larger under a high-temperature condition (12 ºC) than a low-temperature condition (6 ºC), explaining the downstream dominance of white-spotted charr in the longitudinal distribution pattern of the two species. However, under the low-temperature condition, they showed no differences in competitive ability between the two species. That is, upstream dominance of Dolly Varden could not be explained by the superiority in interference behaviour. A similar lack of the superiority of upstream-dominant species has also been reported by some studies (McHugh and Budy

2005; McMahon et al. 2007). Therefore, aspects other than interference interactions for feeding habitat should be considered for better understanding of longitudinal replacement. In addition, studies on condition-specific competition have usually adopted experimental approaches. Controlled experiments are useful to clarify condition-specific differences in behaviour, growth and survival between target species. However, experiments tend to conduct within short-term periods (but Taniguchi and Nakano 2000), and thus, it is difficult to deal with interactions related to ontogenetic or seasonal changes of fish and environments at longer terms. Therefore, long-term monitoring of growth and survival would also be important.

White-spotted charr (*S. l.* subspp.) and masu salmon (*O. m.* subspp.) are common stream salmonids in Japan. Masu salmon are distributed throughout the main four islands of Japan (Hokkaido, Honshu, Shikoku and Kyushu), although white-spotted charr are absent from southwestern regions (Shikoku and Kyushu). In rivers where both species are native, white-spotted charr dominate upper reaches but are replaced by masu salmon downstream (Imanishi 1951; Miyasaka et al. 2003; Morita et al. 2016; Tsuboi et al. 2020). Although such longitudinal replacement between these two species have been considered to be related to longitudinal gradients of water temperature (Imanishi 1951) or current velocity (Nakano 1991; Morita et al. 2016), mechanisms underlying the replacement have not yet been fully explored. In this chapter, I focused on interspecific competition between these two species.

In southwestern Japan where white-spotted charr is not originally distributed (i.e. Shikoku and Kyushu), introduced white-spotted charr populations have established in several streams inhabited by native masu salmon (Kondou et al. 1999; Inoue et al. in press). In one case (Kurokawa River), introduced white-spotted charr has created the common longitudinal pattern (upstream and downstream dominance by white-spotted charr and masu salmon, respectively), by displacing native red-spotted masu salmon in upper reaches (Inoue et al. in press). This displacement of red-spotted masu salmon by white-spotted charr suggests that white-spotted charr would be competitively superior to red-spotted masu salmon in upper headwater reaches of the Kurokawa River. However, Inoue et al. (in press) questioned that "how did white-spotted charr establish and prevail under the competitive pressure from native red-spotted masu salmon?", because white-spotted charr seems to be inferior to masu salmon in the interference competition. Experimental studies by Hasegawa et al. (2004) and Hasegawa and Maekawa (2006) indirectly showed that masu salmon has higher interference competitive ability (for feeding habitat) than white-spotted charr. Furthermore, the spawning season of white-spotted charr is later than that of red-spotted masu salmon (Maruyama 1981; Nakamura 1999). The late spawning of white-spotted charr leads to their smaller body size than red-spotted masu salmon at the fry stage, resulting in competitive disadvantage for white-spotted charr (Lovén Wallerius et al. 2022). Therefore, factors providing competitive advantages to white-spotted charr in upper headwater reaches should be explored to understand mechanisms of the displacement of native red-spotted masu salmon by non-native white-spotted charr (Inoue et al. in press).

In the Kurokawa River, although introduced white-spotted charr has displaced native red-spotted masu salmon in upper reaches, some headwater reaches harbor only red-spotted masu salmon due to impassable barriers (waterfalls and dams) that prevent upstream colonisation by white-spotted charr. Such a situation provides a unique opportunity for studying interactions between the two species. In rivers where both species are native, it is difficult to investigate the ecology of masu salmon in headwater reaches, because white-spotted charr dominate there. In the Kurokawa River, comparative studies on ecological characteristics of the two species in headwater reaches can be conducted, owing to the above-barrier reaches without white-spotted charr.

Here, I explored two possible mechanisms of displacement of red-spotted masu salmon by white-spotted charr in upper reaches of the Kurokawa River. One is redd superimposition, which may offer an advantage to later-spawning white-spotted charr. I examined potential of redd superimposition in relation to stream size (i.e. longitudinal gradient). Another is related to differences in growth. I monitored growth and persistence of the two species to examine competitive effects of white-spotted charr on red-spotted masu salmon.

3-1. Overlap in spawning habitat characteristics between two salmonids in relation to stream size: redd superimposition hypothesis on longitudinal species replacement

3-1-1. Introduction

Redd superimposition, spawning on a previous spawner's redd by a later spawner, has been recognised as a form of intra- and inter-specific competition in salmonids (Hayes 1987; Essington et al. 2000). Redd superimposition damages eggs and fry in redds, and reduces reproductive success of previous spawners. For example, in a New Zealand stream, Hayes (1987) experimentally showed that survival rates of brown trout (*Salmo trutta*) eggs were reduced by 94% through redd superimposition by rainbow trout (*Oncorhynchus mykiss*), of which spawning season is later than that of brown trout. Furthermore, he also showed that, within the rainbow trout population, the relative reproductive success of late spawners was approximately 50 times higher than that of early spawners. As in New Zealand, non-native salmonids have been introduced in many regions of the world, and displacement of native by non-native salmonids have frequently been reported (e.g. Waters 1999; Fausch 2008; Morita 2018). Although mechanisms underlying such species displacement have not always been clarified, redd superimposition can be one potential mechanism for the displacement when the spawning season of an introduced salmonid species is later than that of native salmonids. In fact, some authors have raised concerns about negative effects of non-native on native salmonids through redd superimposition (Taniguchi et al. 2000; Nomoto et al. 2010).

High rates of redd superimposition may be attributable to low availability of spawning habitat relative to spawner abundance (Beard and Carline 1991; Ligon et al. 1995). However, Essington et al. (1998) and Gortázar et al. (2012) found high rates (> 50%) of redd superimposition in brook trout (*Salvelinus fontinalis*) and brown trout (mainly intraspecific superimposition) even when the density of spawners or redds was low, suggesting that spawners tended to prefer pre-existing redd sites. On the other hand, their data also showed that redd superimposition rate was always high when the density of spawners or redds was high (Essington et al. 1998; Gortázar et al. 2012), suggesting that redd superimposition was inevitable in their study reaches with low habitat availability relative to spawner abundance. These studies suggest that, although the frequency of redd superimposition cannot be explained simply by habitat availability alone, space limitation is a fundamental cause of redd superimposition. Regarding interspecific superimposition, within-reach habitat variation may be especially important. Suitable spawning habitat for salmonids is generally characterised as a streambed dominated by gravel and pebbles free from fine sediments with moderate current (Bjorn and Reiser 1991). However, detailed habitat preference differs among species to some extent, and interspecific spatial segregation of spawning-site use has frequently been observed (e.g. Witzel and MacCrimmon 1983; Fukushima and Smoker 1998; Geist et al. 2002). Such interspecific differences in spawning-habitat preference may mitigate the occurrence of interspecific redd superimposition. However, in stream channels where habitat variation is limited, the opportunity for interspecific spatial segregation would also be limited. Therefore, smaller channels with lower habitat variation would have higher potential for redd superimposition.

In stream systems, channel width, water depth and current velocity increase downstream (Church 1992; Allan 1995). This indicates that variations in habitat characteristics (e.g. range of depth and velocity), as well as habitat space, decrease upstream as channel size becomes smaller. Accordingly, habitat availability for fishes would also decrease upstream. Furthermore, upstream increases (or negative correlations with channel size) of the density of stream salmonids have frequently been observed (Bozek and Rahel 1991; Inoue and Nakano 1998; Rosenfeld et al. 2000; Sweka and Mackey 2010; Inoue et al. 2013). These facts suggest that the occurrence potential of redd superimposition would increase upstream, and thereby providing competitive advantage to later-spawning species in upper, smaller streams. However, little attention has been paid to such a possible longitudinal change in redd superimposition potential and its concomitant effects on the competitive advantage in interspecific interactions.

Longitudinal species replacement has often been reported for various pairs of stream salmonids, such as Dolly Varden and white-spotted charr (Fausch et al. 1994), bull char and rainbow trout, cutthroat trout and rainbow trout (Reeves et al. 2011), and white-spotted charr and masu salmon (Miyasaka et al. 2003). Condition-specific competition, in which competitive superiority changes along longitudinal gradients, has often been considered an underlying mechanism of such longitudinal replacement (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000; McMahon et al. 2007). Most previous studies on condition-specific competition in salmonids have focused on interference interactions for feeding habitat (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000; McMahon et al. 2007), probably because stream salmonids are famous for their territorial feeding behaviour in a dominance hierarchy (e.g. Fausch 1984; Nakano 1995a, b). Consequently, other aspects of interspecific interactions, such as reproductive phase, have rarely been considered as a causal mechanism of longitudinal species replacement.

White-spotted charr and masu salmon are common stream salmonids in Japan. Masu salmon are distributed throughout the main four islands of Japan (Hokkaido, Honshu, Shikoku and Kyushu), although white-spotted charr are absent from southwestern regions (Shikoku and Kyushu). In rivers where both species are native, white-spotted charr dominate upper reaches but are replaced by masu salmon downstream (Imanishi 1951; Miyasaka et al. 2003; Morita et al. 2016; Tsuboi et al. 2020). Although such longitudinal replacement between these two species have been considered to be related to longitudinal gradients of water temperature (Imanishi 1951) or current velocity (Nakano 1991; Morita et al. 2016), mechanisms underlying the replacement have not yet been fully explored. In southwestern Japan where white-spotted charr is not originally distributed (i.e. Shikoku and Kyushu), introduced white-spotted charr populations have been established in several streams inhabited by native masu salmon (Kondou et al. 1999; Inoue et al. in press). In one case (Kurokawa River), introduced white-spotted charr has created the common longitudinal pattern (upstream and downstream dominance by white-spotted charr and masu salmon, respectively), by displacing native masu salmon in upper reaches (Inoue et al. in press). This situation provides a unique opportunity to investigate effects of abiotic and biotic factors on the formation of their distribution pattern.

In the Kurokawa River in Shikoku Island, introduced white-spotted charr was first recorded in 1998 (Mizuno 2000; Yamamoto and Doi 2000). This non-native charr had expanded its distribution and established its upstream dominance by displacing native red-spotted masu salmon by 2014 (i.e. the common longitudinal pattern was created) (Inoue et al. in press). This situation suggests that white-spotted charr would be competitively superior to red-spotted masu salmon in upper headwater reaches of the Kurokawa River. However, Inoue et al. (in press) questioned that “how did white-spotted charr establish and prevail under the competitive pressure from native red-spotted masu salmon?”, because white-spotted charr seems to be inferior to masu salmon in the interference competition. Experimental studies by Hasegawa et al. (2004) and Hasegawa and Maekawa (2006) indirectly showed that masu salmon has higher interference competitive ability (for feeding habitat) than white-spotted charr. Furthermore, the spawning season of white-spotted charr is later than that of red-spotted masu salmon (Maruyama 1981; Nakamura 1999). The late spawning of white-spotted charr leads to their smaller body size than red-spotted masu salmon at the fry stage, resulting in competitive disadvantage for white-spotted charr (Lovén Wallerius et al. 2022). Therefore, factors providing competitive advantages to white-spotted charr in upper headwater reaches should be explored to understand mechanisms of the displacement of native red-spotted masu salmon by non-native white-spotted charr (Inoue et al. in press). Also, this would contribute to better understanding of the longitudinal species replacement in salmonids in general.

As discussed earlier, late spawning has an advantage in reproductive success through redd superimposition. Inoue et al. (in press) showed that the dominance of non-native white-spotted charr was more clearly related to stream size than elevation (a proxy for water temperature), suggesting that smaller channel size rather than lower water temperature may have facilitated the charr dominance in the Kurokawa River. If the frequency of redd superimposition increases upstream, late-spawning white-spotted charr would have an advantage over red-spotted masu salmon in small upper reaches. In this study, I explored whether the dominance of non-native white-spotted charr (displacement of native red-spotted masu salmon) in upper reaches of the Kurokawa River can be explained by redd superimposition. I hypothesised that smaller channels of upper reaches would have higher potential of redd superimposition, thereby providing a competitive advantage to later-spawning white-spotted charr. I examined following predictions: 1) availability of spawning habitat would decrease upstream according to channel size, and 2) overlap in spawning habitat characteristics between the two species would increase upstream owing to the decrease of habitat availability.

3-1-2. Materials and methods

Study area

The Kurokawa River is a tributary of the Niyodo River, in Shikoku Island, southwestern Japan (Fig.3-1.1). The study area is located between 800 and 1000 m in elevation, with annual precipitation ranging from 2000 to 3000 mm. Although potential vegetation is deciduous broadleaved forest, the study area is dominated by plantations of evergreen conifers. Native fat minnow, in addition to red-spotted masu salmon and the introduced white-spotted charr, is distributed in this area. Both red-spotted masu salmon and white-spotted charr in this area are stream-resident (non-anadromous) populations. Although the non-native white-spotted charr had expanded their distribution throughout this area by 2014, a sediment control dam and natural waterfalls had prevented their upstream colonisation (Inoue et al. in press). As a result, there remained some tributaries of which uppermost reaches harbored only red-spotted masu salmon.

I established nine survey sections (section length: 270 – 920 m) to quantify characteristics and availability of spawning habitat of the two species at different longitudinal positions (different channel size) (Fig.3-1.1, Table 3-1.1). Using catchment area as an index of channel size, the survey sections were classified into three classes, small-sized (catchment area < 1 km^2), middle-sized (1–10 km^2), and large-sized channels (> 10 km^2) (catchment area: 0.3-30.8 km^2; wetted width: 1-13 m; Table 3-1.1). Two of the nine sections were inhabited only by red-spotted masu salmon (i.e. above a dam or a waterfall: SC3 and MC4; Fig.3-1.1, Table 3-1.1), whereas other sections had both species. In regions where both species are native (e.g. Honshu, central Japan), habitat characteristics of masu salmon in small headwater streams are generally difficult to survey, because such small channels in upper reaches are dominated by white-spotted charr. Similarly, in the study area, red-spotted masu salmon was scarce in small headwater streams where the non-native white-spotted charr population had been established. However, headwater reaches without white-spotted charr above barriers (dam or waterfall) allowed us to investigate characteristics of spawning habitat of red-spotted masu salmon in such small streams, which is a strength of this study.

Field survey

Characteristics and availability of spawning habitat of white-spotted charr and red-spotted masu salmon were surveyed in autumn of 2019 and 2020. To detect their spawning habitats, each survey section was visited twice per week during the periods from10 October to 28 November in 2019 and from 30 September to 21 November in 2020. Although all the nine sections were surveyed in 2020, four of the nine sections were not surveyed in 2019 (i.e. the four sections were added in 2020) (Table 3-1.1). When a spawning behaviour was observed, I recorded spawner species and marked the position of the redd by putting a marker near the redd. When a redd with no spawner was found, spawner species was identified on the basis of the date of the finding. In both years, white-spotted charr spawned later than red-spotted masu salmon (see Results: Fig.3-1.2, Table S3-1.1). Spawning behaviour of red-spotted masu salmon and white-spotted charr was observed during the periods from 22 October to 1 November and 30 October to 21 November in 2019, respectively, and from 2 to 28 October and 20 October to 5 November in 2020, respectively. These spawning periods of the two species seldom overlapped within each section in both years (Table S3-1.1).

Characteristics of their spawning habitat were represented by water depth, current velocity and substrate composition at each redd site. Water depth (cm) and current velocity ($cm \cdot s^{-1}$) were measured at the dome of each redd. Current velocity at the surface, mid-depth (0.6 depth), and bottom were measured using a portable current metre (CKK-VR301, KENEK), and mean current velocity was calculated. The substrate surface within a 900-cm^2 area on each redd was assessed using a grid frame (30 × 30 cm), which included 25 quadrats on a 6×6 cm grid. The substrate type within each quadrat was classified as bedrock, sand (dominant particle size < 2 mm), gravel (2 – 16 mm), pebble (17 – 64 mm), cobble (65 – 256 mm) or boulder (> 256 mm). The percent frequency of gravel and pebbles within the 900-cm^2 area was used as a variable representing substrate characteristics, because most redds of both species were found on gravel-pebble substrates. To quantify availability of spawning habitat, a representative survey reach (length; 30 – 160 m) was established in each survey section. The location and length of the survey reaches were determined so as to include areas where redds were frequently observed and to include multiple pool-riffle sequences. In the survey reaches, 20 – 30 transects were established at 1 – 8 m intervals along the stream, depending on stream size (intervals of 0.5 – 1.0 wetted width of each reach). Along each transect, measuring points were set at equal intervals (0.3 –3.0 m: interval of < 0.25 wetted width). Water depth, current velocity and substrate were quantified at each point in the same manner as the measurements of spawning habitat characteristics.

Statistical analysis

To examine whether the availability of spawning habitat decreased upstream according to channel size, frequency distributions of availability measurements for water depth, current velocity and the percentage of gravel and pebbles were compared between large- and middle-sized channels, and middle- and small-sized channels, using Kolmogorov-Smirnov test. To examine whether the degree of overlap in spawning habitat characteristics between the two species differed among the three channel-size classes, permutational multivariate analysis of variance (PERMANOVA) and Pianka's overlap index (Pianka 1973) were used. Within each channel-size class, water depth, current velocity and the percentage of gravel and pebbles at redd sites were compared between the two species by PERMANOVA with statistical values using 999 permutations. Pianka's overlap index was used to express the overlap degree in each spawning-habitat variable between the two species. To calculate Pianka's overlap index, each variable was expressed by discrete values by dividing class intervals as: 10 cm, 10 $\text{cm}\cdot\text{s}^{-1}$, and 10 % for water depth, current velocity and the percentage of gravel and pebbles, respectively. Pianka's index was described as:

$$\alpha_{sc} = \frac{\sum_h P_{sh} P_{ch}}{\sqrt{(\sum_h P_{sh}^2)(\sum_h P_{ch}^2)}}$$

where α_{sc} = Pianka's index between red-spotted masu salmon (s) and white-spotted charr (c), P_{sh} and P_{ch} = the proportion of class h for red-spotted masu salmon and white-spotted charr, respectively. In these analyses, the data were pooled for each channel size class. All statistical analyses were conducted in R version 4.1.1 (R Core Team 2021).

3-1-3. Results

A total of 128 and 151 redds of white-spotted charr and red-spotted masu salmon, respectively, were recorded during the two-year survey (Table 3-1.1). In both years, redds of red-spotted masu salmon were first found in October, followed by those of white-spotted charr (Fig. 3-1.2, Table S3-1.1). In streams inhabited by both species, redds of red-spotted masu salmon were more abundant than those of white-spotted charr in the large-sized channels (77 versus 29) and *vice versa* in the small-sized channels (8 versus 38), reflecting their longitudinal distribution (Table 3-1.1, Table S3-1.1). Neither intra- nor interspecific redd superimposition was found during the survey.

The availability of their spawning habitat differed by the channel size (Fig.3-1.3). Kolmogorov-Smirnov tests comparing the frequency distribution of the availability measurements showed that both water depth and current velocity differed between large- and middle-sized channels (P = 0.001 for depth, P = 0.007 for velocity), and also between middle- and small-sized channels (P = 0.001 for both depth and velocity). The distributions of water depth and current velocity shifted toward shallower and slower directions as channel size decreased from large- to small-sized channels (Fig. 3-1.3). The reduction of habitat availability or variation according to channel size was also clearly shown by the scatter plots of current velocity and water depth (Fig. 3-1.4): the range of water depth and current velocity became narrower as the channel size decreased. The availability for the percentage of gravel and pebbles did not significantly differ between large- and middle-sized channels ($P = 0.186$), whereas differed between middle- and small-sized channels ($P = 0.011$) (Fig.3-1.3).

White-spotted charr and red-spotted masu salmon exhibited similar use of spawning habitat in terms of substrate (Fig. 3-1.3). Substrates of most redd sites of both species were dominated by gravel and pebbles (> 90%) in all of the large-, middle-, and small-sized channels. However, PERMANOVA showed significant differences in characteristics of spawning habitat between the two species in large- ($P = 0.001$) and middle-sized channels ($P = 0.001$), although no significant difference was found in small-sized channels ($P = 0.311$) (Fig.3-1.4). In large- and middle-sized channels, red-spotted masu salmon used faster current than white-spotted charr (Fig. 3-1.3, 3-1.4). While more than 80% of white-spotted charr used current velocity lower than 20 $\mathrm{cm \cdot s^{-1}}$, more than 70% of red-spotted masu salmon used current velocity higher than 20 $\mathrm{cm \cdot s^{-1}}$. In small-sized channels, however, most red-spotted masu salmon used current velocity lower than 20 $\mathrm{cm \cdot s^{-1}}$ in accordance with the limited availability of higher velocity there. As a result, frequency distribution of current velocity used by the two species was similar to each other (Fig. 3-1.3). This change in the overlap degree according to channel size was clearly shown by Pinaka's index (Fig. 3-1.5). This overlap index for current velocity was low in large- and middle-sized channels, but sharply increased in small-sized channels. On the other hand, the index values for water depth and the percentage of gravel and pebbles were high regardless of the channel size.

3-1-4. Discussion

My analyses showed that 1) the availability of spawning habitat decreased upstream as channel size decreased, especially in terms of water depth and current velocity, and 2) characteristics of spawning habitat, especially current velocity, highly overlapped between white-spotted charr and red-spotted masu salmon in small-sized channels, whereas those differed between the two species in middle- and large-sized channels. These results are consistent with my predictions, and support my hypothesis that smaller channels of upper reaches would have higher potential of redd superimposition, thereby providing a competitive advantage to later-spawning white-spotted charr.

Preference for spawning habitat has been examined for many salmonid species (e.g. Fukushima 2001; Louhi et al. 2008), and interspecific spatial segregation in spawning habitat has frequently been reported (e.g. Witzel and MacCrimmon 1983; Fukushima and Smoker 1998; Geist et al. 2002). Differences in spawning-site use between white-spotted charr (*S. l.* spp.) and masu salmon (*O. m.* spp.) have also been well described in streams where both species are native (Honshu, central Japan: Maruyama 1981; Nakamura 1999; Kishi et al. 2016; Kishi and Tokuhara 2018). Although both species prefer gravel-pebble substrates, white-spotted charr uses slower current (< 20 cm s^{-1}) than masu salmon (Maruyama 1981; Nakamura 1999; Kishi and Tokuhara 2018). Both Maruyama (1981) and Nakamura (1999) pointed out that interspecific redd superimposition between the two species would rarely occur owing to the distinct differences in their spawning-habitat preference. My results in large- and middle-sized channels are fully consistent with the previous knowledge (Maruyama 1981; Nakamura 1999; Kishi and Tokuhara 2018). However, a high overlap of spawning-habitat characteristics between the two species found in small-sized channels opposes the previous findings. This is a unique aspect of my study.

In regions where both white-spotted charr and masu salmon are native, white-spotted charr mainly uses small upper tributaries as spawning habitat, whereas masu salmon tends to use main stems (Nakamura 1999; Kishi et al. 2016), according to their longitudinal distributions. For example, Kishi et al. (2016) surveyed distribution of spawning sites of the two species over a wide area (ca. 50-km^2 area including tributaries of five river systems) in Hida region, central Honshu, Japan, and reported that wetted width at spawning sites of white-spotted charr and masu salmon ranged from 0.8 to 5.0 m ($N = 90$) and 1.4 to 7.7 m ($N = 59$), with the interquartile range being ca. 1.5-2.9 m and 2.5-4.2 m, respectively. That is, spawning of masu salmon in uppermost headwater reaches is rare, and thus, information on differences (or similarities) in spawning habitat between the two species within small headwater streams has so far been rare. On the other hand, in Shikoku, where white-spotted charr is not distributed naturally, uppermost headwater streams are usually occupied by red-spotted masu salmon (e.g. catchment area < 1 km^2: Inoue et al. 2013; Inoue et al. in press). My results revealed that, in such small streams (catchment area < 1 km^2, wetted width < 2 m, Table 3-1.1), characteristics of spawning habitat of masu salmon highly overlapped with those of white-spotted charr. This overlap in small-sized channels is apparently due to lower habitat availability in small-sized channels than in middle- and large-sized channels. In small-sized channels, red-spotted masu salmon appears to be forced to use slow current, owing to limited availability of fast current (Figs. 3-1.3, 3-1.4). My results suggest that spatial segregation in spawning habitat can be prevented in small streams, even between species having different spawning-habitat preference.

In the Kurokawa River, stream reaches dominated by non-native white-spotted charr (relative abundance > 80%) were generally those with catchment area < 3 km^2 (Inoue et al. in press). However, uppermost reaches (catchment area < 2 km^2) above barriers (dam, waterfall) that had prevented upstream invasion by non-native white-spotted charr maintained high density of red-spotted masu salmon (Inoue et al. in press). Such circumstantial evidence and statistical analyses by Inoue et al. (in press) suggested that, in small headwater tributaries of the Kurokawa River, red-spotted masu salmon had been displaced by non-native white-spotted charr. Although mechanisms underlying this displacement are unclear, selective displacement in small streams suggests that white-spotted charr would have some competitive advantages over red-spotted masu salmon in small headwater streams. Results of the present study suggest that redd superimposition by late-spawning white-spotted charr is one plausible mechanism to account for the displacement by white-spotted charr specific to small streams. Waters (1999) reported displacement of native brook trout by non-native brown trout in a Minnesota stream using long-term data, and pointed out effects of redd superimposition by late-spawning brown trout as a possible cause of the displacement. In New Zealand, elimination of brown trout through redd superimposition by late-spawning rainbow trout in an inlet stream of a reservoir was suggested by Scott and Irvine (2000).

Although my results suggest redd superimposition as a possible mechanism of the displacement by the non-native white-spotted charr in the Kurokawa River, no interspecific redd superimposition was actually observed during the survey periods. This may be due, at least in part, to low densities of red-spotted masu salmon in the small-sized channels where non-native white-spotted charr had invaded; only a few redds of red-spotted masu salmon were found (Table 3-1.1). In the study sections for the small-sized channels, the dominance of white-spotted charr had already been established by the time of my survey. Redd superimposition by non-native white-spotted charr may frequently occur in the initial phase of their invasion. Consequently, the present study could not provide direct evidence of effects of redd superimposition. However, the results supporting my initial hypothesis (higher potential of redd superimposition in upper, smaller channels) encourage future studies, such as experimental re-introduction of redd-spotted masu salmon in the upper reaches dominated by the non-native white-spotted charr, to examine the occurrence and effects of redd superimposition. If redd superimposition by non-native white-spotted charr in the small, upper reaches are found to have substantial effects on re-introduced red-spotted masu salmon, this exclusion mechanism can apply also to the formation of the longitudinal pattern of the two species in regions where both species are native. The longitudinal replacement between white-spotted charr and masu salmon has long been recognized (Imanishi 1951; Kawanabe 1989), and the pattern has been considered to be related to water temperature or current velocity (channel gradient) (Imanishi 1951; Nakano 1991; Morita et al. 2016). My results suggest that also channel size and redd superimposition are worth considering when examining mechanisms underlying the longitudinal pattern of white-spotted charr and masu salmon.

Longitudinal species replacement has interested stream fish ecologists (e.g. Rahel and Hubert 1991; Fausch et al. 1994), and condition-specific competition has been considered a typical mechanism of the longitudinal replacement in salmonids (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000; McMahon et al. 2007). These studies have usually focused on temperature-mediated changes in competitive superiority for feeding habitat, and have successfully shown superiority of downstream-dominant species at higher water temperatures. On the other hand, previous studies have often failed to show superiority of upstream-dominant species (De Staso and Rahel 1994; Taniguchi and Nakano 2000; McMahon et al. 2007), suggesting that other aspects should be considered. My results present a channel-size-mediated change in competitive superiority along longitudinal gradients. This can explain competitive superiority of upstream-dominant species in some cases (i.e. upstream dominance by late-spawning species: e.g. Dolly Varden versus white-spotted charr; white-spotted charr versus masu salmon). So far, little attention has been paid to spawning interactions when examining the causes of longitudinal replacement. My results provide a new perspective on longitudinal changes in competitive advantages in salmonids, although factors other than behavioral aspects should also be considered to better understand mechanisms underlying longitudinal replacement (e.g. growth potential, fecundity: Öhlund et al. 2008).

Table 3-1.1. General descriptions of the survey sections. White-spotted charr was absent from SC3 and MC4.

Channel-size class	Section	Year	Total number of redds: Salmon	Total number of redds: Charr	Section length (m)	Altitude (m)	Catchment area (km^2)	Wetted width (m)
Small-sized channel	SC1	2020, 2019	3	21	540	1020	0.81	1.3
	SC2	2020	5	17	310	930	0.33	1.7
	SC3	2020, 2019	30	—	700	980	0.57	1.8
Middle-sized channel	MC1	2020, 2019	12	32	730	970	1.21	1.9
	MC2	2020	0	9	270	950	1.02	2.6
	MC3	2020, 2019	13	20	650	910	1.09	2.6
	MC4	2020	11	—	760	950	1.96	4.1
Large-sized channel	LC1	2020, 2019	46	8	430	830	11.47	4.9
	LC2	2020	31	21	920	800	30.81	12.9

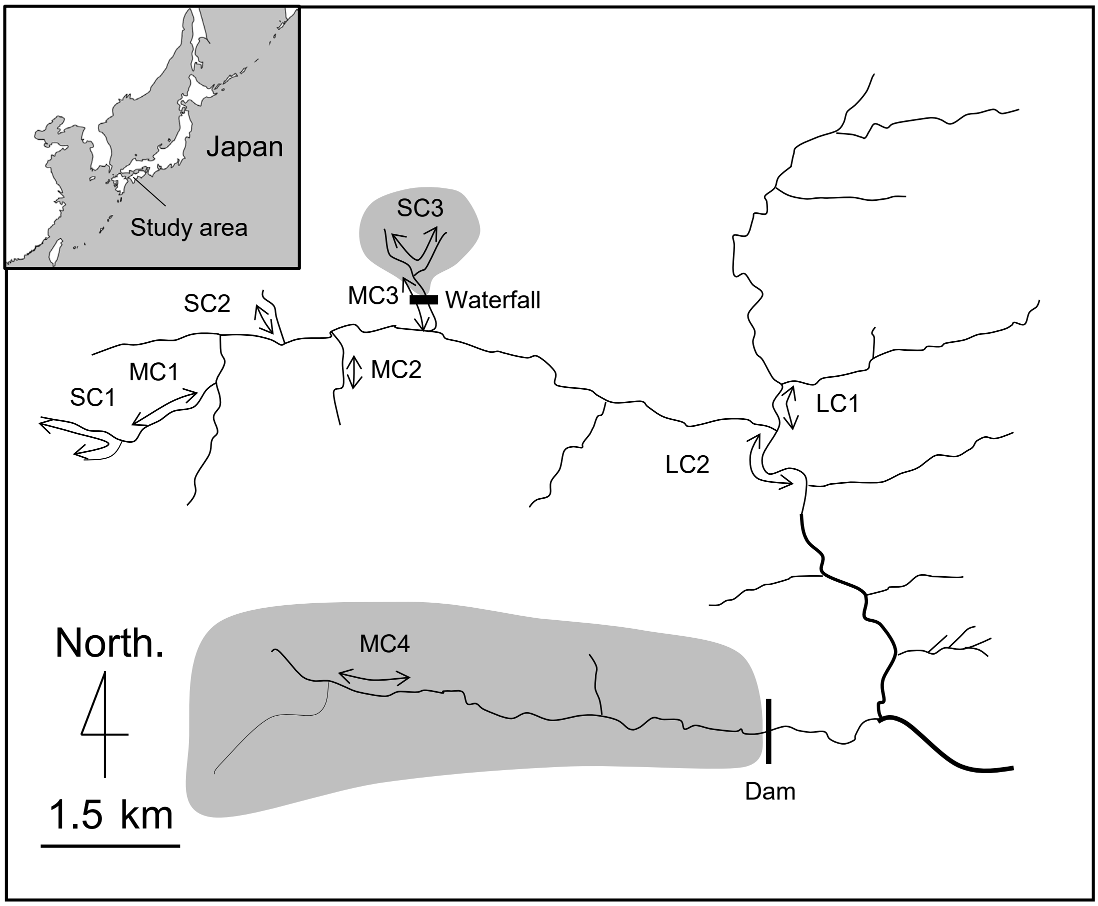

Fig.3-1.1. Map of the study area of the Kurokawa River in southwestern Japan. White spotted charr, which is a non-native species, is absent from the shaded areas, owing to barrier effects by a dam and a waterfall.

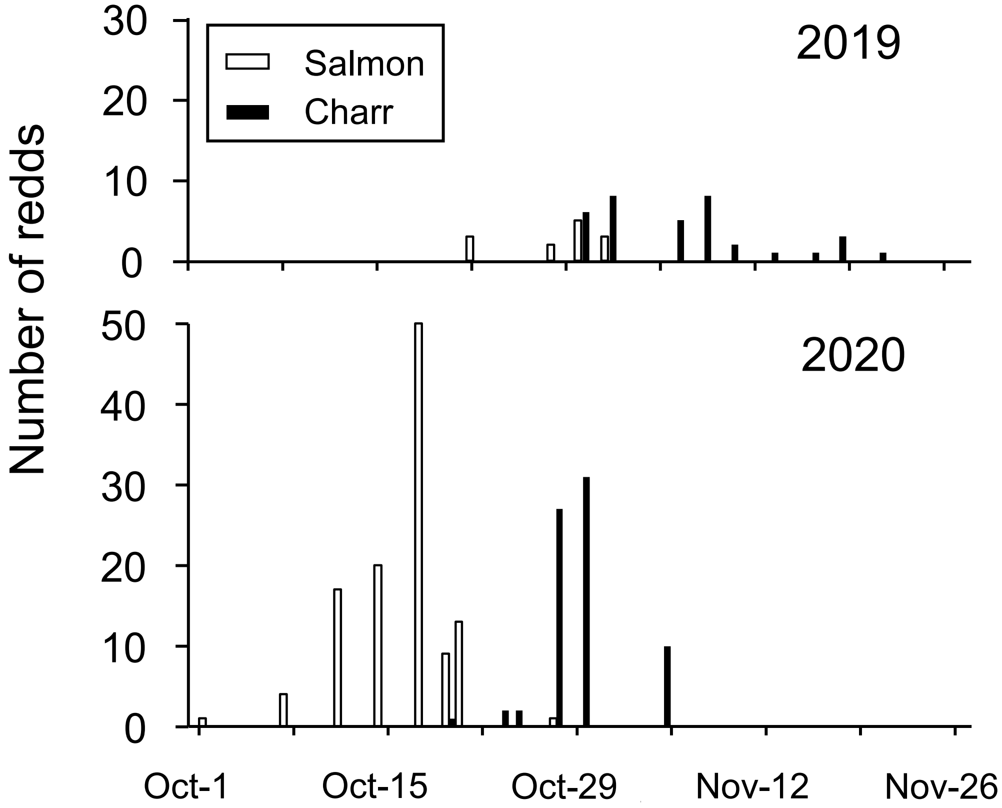

Fig.3-1.2. Number of observed redds of white-spotted charr (solid bar) and red-spotted masu salmon (open bar) during the study periods in 2019 and 2020.

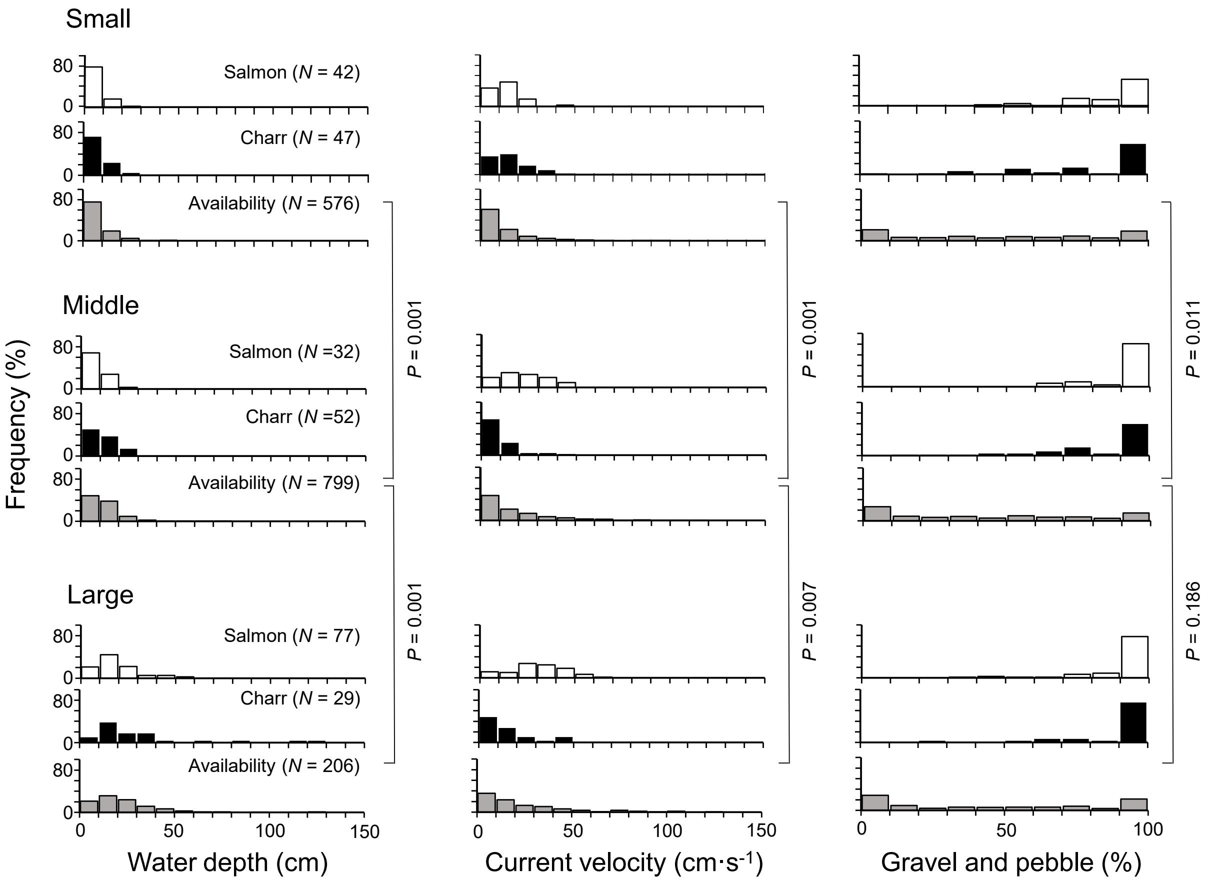

Fig.3-1.3. Frequency distribution of water depth, current velocity and the percentage of gravel and pebble at redds of red-spotted masu salmon (open bar) and white-spotted charr (solid bar), and of spawning-habitat availability (shaded bar), with results of Kolmogorov-Smirnov tests comparing the availability by the channel-size class.

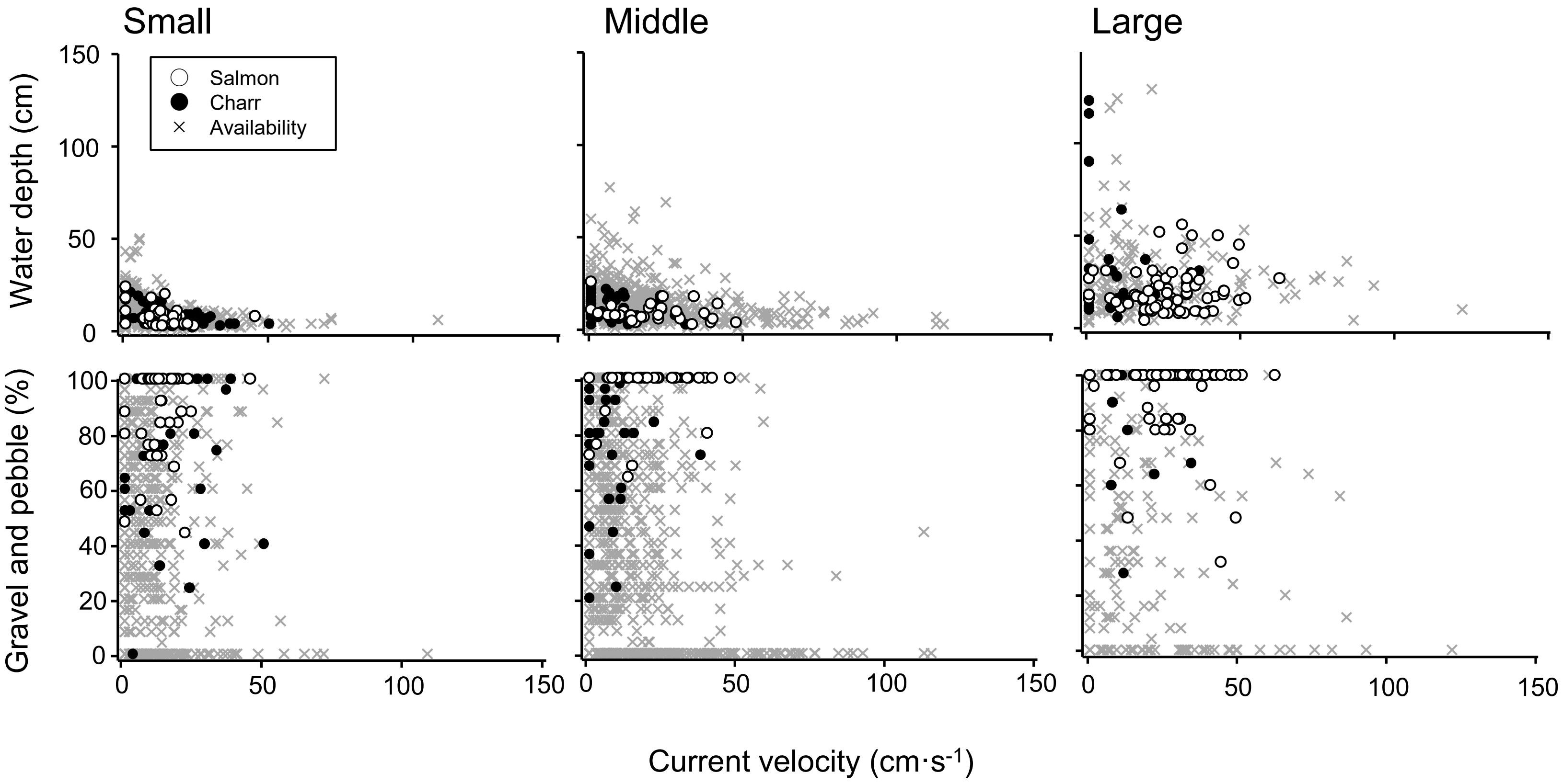

Fig.3-1.4. Distributions of redd sites of red-spotted masu salmon (open circle) and white-spotted charr (solid circle) and spawning-habitat availability (cross) on the scatter plots for the relationships of water depth and percent gravel and pebble with current velocity.

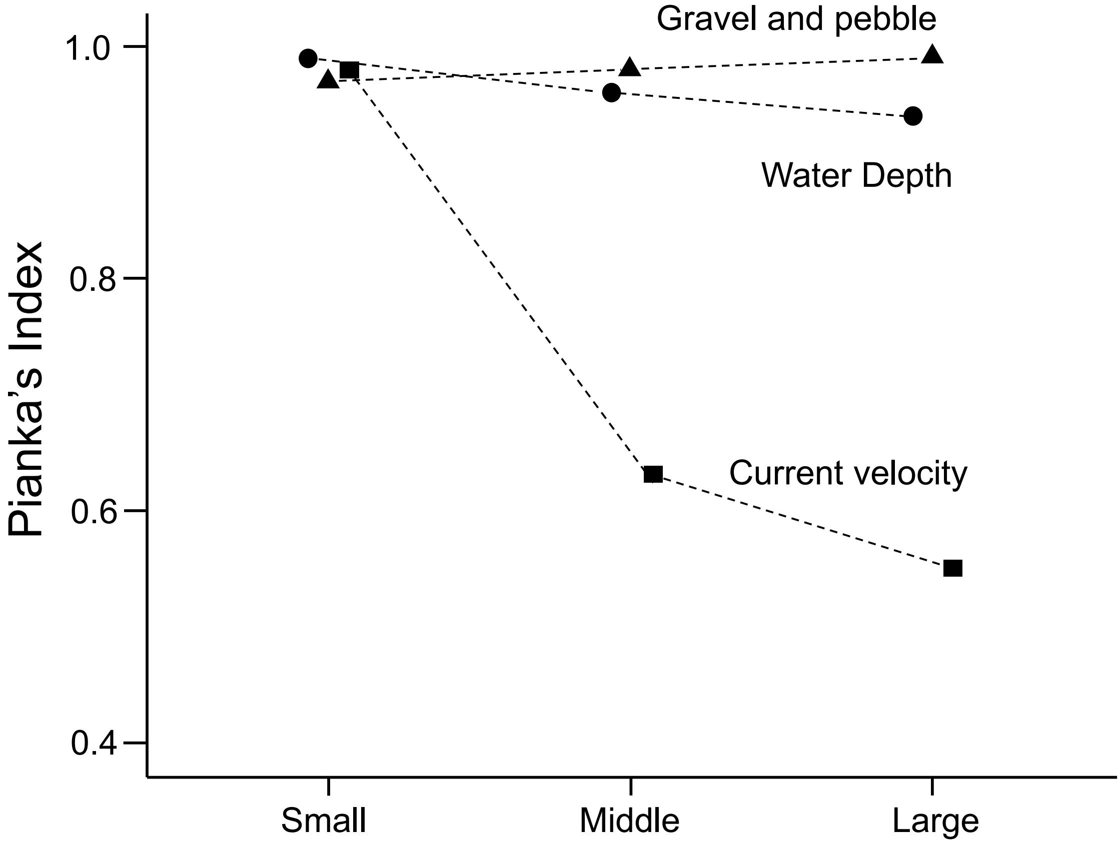

Fig.3-1.5. Pianka's overlap index for water depth (solid circle), current velocity (solid square) and percent gravel and pebble (solid triangle) at redds between red-spotted masu salmon and white-spotted charr in small-, middle-, and large-sized channels.

Table S3-1.1. Number of observed and conjectured redds for white-spotted charr and red-spotted masu salmon in 2019 and 2020 for each section.

			Observed		Conjectured	
	Section	Inhabiting species	Salmon redds	Charr redds	Salmon redds	Charr redds
2019	SC1	Salmon/Charr	0	2 (01Nov-06Nov)	0	0
	SC2	Salmon/Charr	—	—	—	—
	SC3	Salmon	6 (22Oct-01Nov)	0	0	0
	MC1	Salmon/Charr	1 (22Oct)	12 (30Oct-21Nov)	1 (28Oct)	6 (06Nov-21Nov)
	MC2	Salmon/Charr	—	—	—	—
	MC3	Salmon/Charr	0	5 (04Nov-10Nov)	0	5 (01Nov-08Nov)
	MC4	Salmon	—	—	—	—
	LC1	Salmon/Charr	4 (30Oct-01Nov)	3 (18Nov)	4 (30Oct-01Nov)	1 (16Nov)
	LC2	Salmon/Charr	—	—	—	—
2020	SC1	Salmon/Charr	2 (18Oct-20Oct)	18 (28Oct-05Nov)	1 (18Oct)	1 (30Oct)
	SC2	Salmon/Charr	5 (13Oct-16Oct)	17 (28Oct-30Oct)	0	0
	SC3	Salmon	18 (02Oct-21Oct)	0	6 (12Oct-21Oct)	0
	MC1	Salmon/Charr	5 (15Oct-20Oct)	12 (28Oct-05Nov)	5 (15Oct-20Oct)	2 (28Oct-30Oct)
	MC2	Salmon/Charr	0	7 (20Oct-05Nov)	0	2 (30Oct)
	MC3	Salmon/Charr	11 (15Oct-21Oct)	10 (25Oct-05Nov)	2 (15Oct)	0
	MC4	Salmon	9 (12Oct-18Oct)	0	2 (12Oct)	0
	LC1	Salmon/Charr	31 (08Oct-21Oct)	4 (28Oct)	7 (08Oct-18Oct)	0
	LC2	Salmon/Charr	21 (12Oct-28Oct)	15 (28Oct-1Nov)	10 (12Oct-20Oct)	6 (30Oct-05Nov)

3-2. Effects of introduced white-spotted charr on the growth and survival of native red-spotted masu salmon

3-2-1. Introduction

For stream-dwelling salmonids, consequences of interference competition for foraging habitat largely depend on relative body size of competitors, and affect their growth and survival (Nakano 1995a, b, Fausch et al. 2021). In a local habitat, such as a pool, larger individuals are superior to smaller individuals, and can occupy better foraging habitat as their territories (Nakano 1995a, b, Fausch et al. 2021). Smaller individuals that cannot have their territories leave the local habitat (Nakano 1995a). Therefore, size-dependent-dominance hierarchies can strongly affect fish assemblage within each local habitat. During age-0 stage, body size often differs among species due to species-specific differences in spawning timing. The differences, which later-spawning species are more likely to be smaller than earlier-spawning species, result in asymmetric competition, which can cause replacement of later-spawning species by earlier-spawning species (Öhlund et al. 2008; Lovén Wallerius et al. 2022). Thus, considering size-dependent dominance hierarchies, later-spawning species would be inferior to earlier-spawning species during age-0 stage.

Fish growth is largely determined physiologically by environmental conditions such as temperature and flow (Jonsson and Jonsson 2009). Responses of growth to an environmental factor are species-specific, and growth potential in given conditions differs between species. For example, although optimum growth temperature of cutthroat trout and rainbow trout is a similar range (cutthroat trout: 13.6 °C; rainbow trout: 13.1 °C), the range of optimum growth temperature of cutthroat trout is narrower than rainbow trout (Bear et al. 2007). The difference in optimal temperature range leads to higher growth of rainbow trout than cutthroat trout in warmwater temperature (> 22 °C) (Bear et al. 2007). In general, growth of salmonids increases downstream, due to increases in productivity and water temperature (Al-Chokhachy et al. 2022). However, increasing rate of growth along longitudinal environmental gradients can differ among species and the differences can cause longitudinal reversal of body size. Such longitudinal reversal in growth potential between two competing species would affect consequences of their interference competition, and may be a major cause of longitudinal replacement. However, such changes in growth potential have been less considered, when mechanisms underlying species replacement are examined.

In the Kurokawa River, introduced white-spotted charr has displaced native red-spotted masu salmon in upper reaches, despite smaller size of age-0 white-spotted charr, of which spawning season is later than that of red-spotted masu salmon. This displacement suggests that white-spotted charr has advantages to red-spotted masu salmon in upper reaches. I hypothesised that (1) white-spotted charr can grow larger than red-spotted masu salmon in upper reaches, whereas red-spotted masu salmon can grow larger than white-spotted charr in lower reaches and (2) such a longitudinal reversal in body size affects their survival (persistence), resulting in forming longitudinal distribution pattern. I examined whether (1) the longitudinal reversal in growth occurs between white-spotted charr and masu salmon, and (2) white-spotted charr negatively affect growth and persistence of red-spotted masu salmon.

3-2-2. Materials and methods

Study area

The study was conducted in upper reaches of the Kurokawa River, a tributary of the Niyodo River, in Shikoku Island, southwestern Japan (Fig. 3-2.1). The study area is located between 800 and 1000 m in elevation, with annual precipitation ranging from 2000 to 3000 mm. Although potential vegetation is deciduous broadleaved forest, the study area is dominated by plantations of evergreen conifers. Native fat minnow (*Rhynchocypris oxcycephala*), in addition to red-spotted masu salmon and the introduced white-spotted charr, is distributed in this area. Both red-spotted masu salmon and white-spotted charr in this area are stream-resident (non-anadromous) populations. Although the non-native white-spotted charr had expanded their distribution throughout this area by 2014, a sediment control dam and natural waterfalls had prevented their upstream colonisation (Inoue et al. in press). As a result, there remained some tributaries which uppermost reaches harbored only red-spotted masu salmon.

Seventeen study reaches (reach length: 70 – 340 m) were established in two catchments to examine longitudinal trends in growth (body size) of the two species (Fig. 3-2.1). One catchment was inhabited only by masu salmon, because a sediment-control dam installed near the mouth of this tributary had prevented upstream invasion by white-spotted charr. On the other hand, in another catchment, white-spotted charr had widely spread throughout this tributary system except some headwater reaches above impassable waterfalls. The study reaches ranged from 0.4 – 9.0 km^2 in catchment area and 14 –17 °C in summer water temperature (Fig. 3-2.2), with no longitudinal trend being found in water temperature (correlation between water temperature and catchment area: $r = 0.15$, $P = 0.566$). Using these two catchments, I examined differences in longitudinal trends in growth (body size) between the two species and effects of introduced white-spotted charr on the growth and persistence of red-spotted masu salmon.

Field survey

To track growth and persistence of red-spotted masu salmon and white-spotted charr, I conducted mark-recapture survey from early summer in 2020 to midsummer in 2022. In each year, the survey was conducted in three seasons, spring (March), early summer (June) and midsummer (August). Fish individuals were captured by two-pass electrofishing (Model 12 Backpack Electrofisher, Smith-Root Inc.) and fork length (FL) and wet weight were measured. In early summer and midsummer in 2020, captured age-0 individuals were marked with elastomer tag, to track growth and persistence of 2020 cohort. Wetted width of each study reach was measured at 2–5 m intervals to obtain the sampling area (mean wetted width × reach length). The total number of captured individuals divided by the sampling area was used as the density of each species. Summer water temperature was recorded at 1-hours intervals by a data logger (HOBO Temp, Onset) during from 2 to 7 August in 2022 and the mean value was calculated for each reach.

Statistical analysis

I first examined differences in longitudinal trends in body growth among the three population groups, red-spotted masu salmon (allopatric salmon) in allopatric reaches, and red-spotted masu salmon (sympatric salmon) and white-spotted charr (sympatric charr) in sympatric reaches for each survey season. Body growth was represented by FL of 2020 cohort in each survey season, with catchment area above each study reach being used as a longitudinal gradient. Catchment area was measured using Geospatial Information Authority of Japan (GSI) map. I predicted that (1) FL of both species increases downstream, (2) but the increasing rate (slope) of FL along the longitudinal gradient differs among the three populations, and charr grow larger than salmon in upper reaches and *vice versa* in lower reaches. This prediction was tested by a design of analysis of covariance (ANCOVA), with the population group and catchment area as a fixed factor and covariate, respectively. In this ANCOVA, longitudinal reversal of FL between charr and salmon would be detected by an interaction effect of population group and catchment area. Prior to the ANCOVA, effects of catchment area (covariate) on FL were first assessed by significance of correlations. If effects of catchment area are insignificant, one-way analysis of variance (ANOVA) and Tukey-HSD test with population group as a factor was used instead of the ANCOVA.

I also examined differences in between-season growth rate of the 2020 cohort among the three population groups using one-way ANOVA. Between-season growth rate (GR, cm·day^{-1}) in each study reach was expressed as:

$$\mathrm{GR} = \frac{FL_t - FL_{t-1}}{day_t - day_{t-1}}$$

where t is the survey season, day_t is the survey day, and FL_t is the mean FL of 2020 cohort in each reach at day_t.

To examine differences in persistence of the 2020 cohort among the three population groups, the density of each species in each season, its decline between consecutive seasons, and persistence from 2020 were compared using one-way ANOVA with Tukey-HSD tests. The decline of the density (N/100m^2) of 2020 cohort between consecutive seasons was calculated for each study reach as:

$$\text{Decline} = \frac{N_{captured_t} - N_{captured_{t-1}}}{area} \times 100$$

where t is the survey season, where $N_{captured_t}$ is the captured number of the marked individuals in t, where area is the area of each study reach. That is, negative and positive values indicate decline and increase, respectively. Persistence rate (PR) of 2020 cohort at each survey season was calculated for each study reach as:

$$\text{PR} = \frac{N_{captured}}{N_{mark}}$$

where N_{mark} is the number of the marked individuals in 2020 (individuals marked in early summer and midsummer combined) and $N_{captured}$ is the number of the marked individuals captured in each survey season.

I also examined relative importance of effects of intra- and inter-specific competition on growth and persistence of 2020 cohort of each species. Correlation coefficients of mean FL of 2020 cohort of each species with the densities of age > 0 masu salmon, age > 0 white-spotted charr, and total age > 0 fish (masu salmon and white-spotted charr combined) were assessed. If the highest negative correlation is found for the density of opponent species, it would suggest a strong effect of interspecific competition on FL (cumulative growth). Effects of intra- and inter- specific competition on between-season growth rate, between-season decline of density and persistence rate were examined in the same manner. Fork length, density and catchment area were $\log_{10}$–transformed, and persistence rate was arcsine–square–root transformed to standardize variance and improve normality.

3-2-3. Results

Growth of the 2020 cohort

Although correlations of FL with catchment area were positive for all cases (all three populations in every season: Table 3-2.1, Fig. 3-2.3), most of those for masu salmon were insignificant. In contrast, white-spotted charr exhibited significant correlations in most seasons (Table 3-2.1, Fig. 3-2.3). The longitudinal reversal I expected (i.e. white-spotted charr becomes larger than red-spotted masu salmon in upper reaches but *vice versa* in lower reaches) was not observed in any seasons (Fig. 3-2.3). Therefore, FL was simply compared using ANOVA (Table 3-2.2) and Tukey-HSD test. Comparison among the three populations revealed that FL of sympatric salmon was larger than that of allopatric salmon across all seasons (Fig. 3-2.3, 3-2.4). On the other hand, differences in FL between sympatric charr and sympatric salmon changed as they grew larger (Fig. 3-2.4). During age 0, FL of sympatric charr was smaller than that of sympatric salmon (Fig. 3-2.4). However, sympatric charr had caught up in size with sympatric salmon in spring at age 1 and outcompeted in early summer at age 2 (Fig. 3-2.4). Analysis of variance detected differences in between-season growth rate among the three populations during four periods, from early summer to midsummer at age 0, from the latter to spring at age 1, from the latter to early summer at age 1 and from spring to early summer at age 2 (Fig. 3-2.4, Table 3-2.3). The differences during three periods, from early summer to midsummer at age 0, from the latter to spring at age 1 and from the latter to early summer at age 1, were characterised by higher growth of sympatric charr than sympatric salmon and allopatric salmon (Fig. 3-2.4). On the other hand, during from spring to early summer at age 2, the difference was characterised by lower growth of sympatric salmon than sympatric charr and allopatric salmon (Fig. 3-2.4).

Correlation analysis showed that FL of both species was affected by conspecific density, rather than opponent density (Fig. 3-2.5, 3-2.6). Across all survey seasons, negative correlations between FL of masu salmon and salmon density were detected, although FL of masu salmon was not negatively correlated with charr density and total density (Fig. 3-2.5). Negative correlations between FL of sympatric charr and charr density were detected in four survey seasons (midsummer at age 0, early summer at age 1, and spring and midsummer at age 2), although FL of sympatric charr was not negatively correlated with salmon density (Fig. 3-2.6). Also, correlation analysis showed negative correlations between growth rates of both species and conspecific density (Fig. 3-2.7, 3-2.8). Between-season growth rate of masu salmon was negatively correlated with salmon density for two periods, from early summer to midsummer at age 0 and from early summer to midsummer at age 1 (Fig. 3-2.7). Between-season growth rate of sympatric charr was also negatively correlated with charr density during from early summer to midsummer at age 0 (Fig. 3-2.8). On the other hand, between-season growth rates of both species were not negatively correlated with density of the opponent species (Fig. 3-2.7, 3-2.8). Thus, negative effects of conspecific density on growth of both species were detected, whereas no negative effects of density of the opponent species were detected across survey seasons. These results suggest that growth of the both species would be affected more by intraspecific competition, rather than by interspecific competition.

Persistence of the 2020 cohort

Density of the 2020 cohort of allopatric salmon was significantly higher than that of sympatric salmon and sympatric charr across all survey seasons (Fig. 3-2.9, Table 3-2.4). Decline of density of allopatric salmon was significantly larger than those of sympatric salmon and sympatric charr during from age 0 to spring at age 1 (Fig. 3-2.9, Table 3-2.5). Comparison of persistence rates among the three populations showed that persistence rate of sympatric salmon was significantly higher than those of sympatric charr and allopatric salmon in spring at age 1. On the other hand, after spring at age 1, persistence rate of sympatric salmon decreased steeply and no differences in persistence rate among the three populations were detected (Fig. 3-2.10, Table 3-2.6). Although decline of density of masu salmon was not negatively correlated with salmon density and total density across survey seasons, that was negatively correlated with charr density during from spring to early summer at age 1 (Fig. 3-2.11). Decline of density of charr was negatively correlated only with total density during from early summer to midsummer at age 2, not with salmon density and charr density (Fig. 3-2.12). These results suggest that persistence of masu salmon was negatively affected more by interspecific competition, rather than by intraspecific competition, and effects of introduced white-spotted charr on red-spotted masu salmon became higher after spring at age 1.

3-2-4. Discussion

The results did not support my longitudinal growth reversal hypothesis. However, my three-year monitoring survey revealed that white-spotted charr has higher growth rate than masu salmon throughout the longitudinal range of my study sites (Fig. 3-2.3). Although white-spotted charr was smaller than red-spotted masu salmon at age-0 stage, white-spotted charr caught up in size by the summer at age 1, and further outcompeted red-spotted masu salmon during the age-2 stage. In addition, the patterns of density decline and growth of sympatric red-spotted masu salmon during the three years suggest that white-spotted charr negatively affected red-spotted masu salmon in persistence at age 1 and in growth at age 2. Overall, my results suggest that non-native white-spotted charr was able to establish its population under the competitive pressure of native red-spotted masu salmon, owing to its higher growth rate despite smaller size at age-0 stage.

In my study sites, mean FL of white-spotted charr in early summer at age 0 was about 5.9 cm, which was far smaller than sympatric red-spotted masu salmon (ca. 7.3 cm) (Fig. 3-2.3, 3-2.4). However, white-spotted charr grew rapidly from midsummer at age 0 to spring at age 1, and sympatric charr caught up in size with sympatric salmon in spring at age 1. The higher winter growth of white-spotted charr than red-spotted masu salmon suggests that white-spotted charr has some advantages over red-spotted masu salmon in winter. Because white-spotted charr adapts to cold environments more than red-spotted masu salmon, white-spotted charr may be able to grow higher than red-spotted masu salmon under cold water conditions. Furthermore, in their sympatric areas, white-spotted charr feed on benthic invertebrates, whereas red-spotted masu salmon specialise in drifting terrestrial invertebrates (Nakano 1995b, Miyasaka et al. 2003). In winter, benthic invertebrates are abundant, while terrestrial invertebrate inputs are less in river systems (Nakano and Murakami 2001). Therefore, white-spotted charr can be advantageous in feeding over red-spotted masu salmon due to the differences in feeding conditions.

For allopatric salmon and sympatric charr, population regulation by density-dependent mortality due to carrying capacity seemed to be completed in spring at age 1 (Fig. 3-2.9). On the other hand, density of sympatric salmon continued to decline even after spring at age 1 (Fig. 3-2.9). From spring to early summer at age 1, decline of red-spotted masu salmon density was negatively correlated with white-spotted charr density (Fig, 3-2.12). The period from spring to early summer at age 1 was the timing when sympatric charr caught up in size with sympatric salmon, suggesting that white-spotted charr with high winter growth may outcompete native red-spotted masu salmon. Furthermore, growth of sympatric salmon was lower than that of allopatric salmon during from spring to early summer at age 2, when sympatric charr became larger than sympatric salmon in FL. These results suggest that white-spotted charr negatively affected growth and persistence of red-spotted masu salmon after age 1.

Considering their size-dependent dominance hierarchies (Nakano 1995b), white-spotted charr seem to be inferior to red-spotted masu salmon in interference competition, because body size of later-spawning white-spotted charr is smaller than red-spotted masu salmon at age 0. However, in the study area, small white-spotted charr grew larger than red-spotted masu salmon after age 1. This higher growth rate would be a major cause of invasion success of white-spotted charr in the study area. However, it is unclear how small individuals of white-spotted charr survived at age 0 and caught up with red-spotted masu salmon in size at age 1. In the study area, age-0 individuals of white-spotted charr were often caught in woody debris jams where red-spotted masu salmon was rarely caught. Such differences in habitat use between the two species can reduce their interference competition. Therefore, the differences in habitat use may be one possible mechanism of survival of white-spotted charr during the age-0 stage. Future studies need to clarify how age-0 white-spotted charr survive and grow in spite of smaller body size than red-spotted masu salmon. This can contribute to better understanding of dominance of white-spotted charr in upper reaches.

In the study river, although negative effects of white-spotted charr on growth and survival of red-spotted masu salmon were detected, FL of sympatric salmon was larger than allopatric salmon, because FL of red-spotted masu salmon was determined more by conspecific density, rather than white-spotted charr density, across all survey seasons (Fig. 3-2.11). Furthermore, week intraspecific competition due to low salmon density in sympatric reaches led to higher persistence rate of sympatric salmon than those of sympatric charr and allopatric salmon at first overwintering (i.e. in spring at age 1) (Fig. 3-2.10). These results suggest that short-term experiments may fail to detect the disadvantages of red-spotted masu salmon. My three-year monitoring suggests that superiority of some species cannot be explained by short-term growth and persistence, and long-term field survey would be effective for detection of their superiority.

Table 3-2.1. Correlation coefficients (Pearson's r) of FL of the three populations with catchment area for each survey season. Significant correlations are underlined.

		Allopatric salmon		Sympatric salmon		Charr	
Age	Season	r	P	r	P	r	P
0+	Early summer	0.11	0.793	0.22	0.310	0.22	0.576
	Midsummer	0.46	0.247	0.45	0.226	0.77	0.015
1+	Spring	0.66	0.077	0.34	0.372	0.64	0.065
	Early summer	0.52	0.184	0.74	0.023	0.94	< 0.001
	Midsummer	0.60	0.118	0.40	0.281	0.85	0.004
2+	Spring	0.67	0.072	0.55	0.126	0.81	0.008
	Early summer	0.73	0.039	0.61	0.082	0.89	0.001
	Midsummer	0.43	0.284	0.38	0.395	0.88	0.009

Table 3-2.2. Results of one-way ANOVA for differences in FL among the three populations for each survey season. Significant differences are underlined.

		Fork length	
Age	Season	*F*	*P*
0+	Early summer	17.5	< 0.001
	Midsummer	11.2	< 0.001
1+	Spring	11.0	< 0.001
	Early summer	20.3	< 0.001
	Midsummer	21.6	< 0.001
2+	Spring	20.9	< 0.001
	Early summer	20.4	< 0.001
	Midsummer	21.5	< 0.001

Table 3-2.3. Results of one-way ANOVA for differences in between-season growth rate among the three populations for each survey period. Significant differences are underlined.

		Growth rate	
Age	Period	*F*	*P*
0+	Early summer – Midsummer	4.2	0.028
	Midsummer – Spring	16.3	< 0.001
1+	Spring – Early summer	5.1	0.015
	Early summer – Midsummer	3.3	0.056
	Midsummer – Spring	0.3	0.725
2+	Spring – Early summer	10.7	< 0.001
	Early summer – Midsummer	0.3	0.783

Table 3-2.4. Results of one-way ANOVA for differences in density of 2020 cohort among the three populations for each survey season. Significant differences are underlined.

		Density of 2020 cohort	
Age	Season	*F*	*P*
0+	Early summer	7.9	0.002
	Midsummer		
1+	Spring	4.2	0.028
	Early summer	6.2	0.007
	Midsummer	6.0	0.008
2+	Spring	9.8	0.001
	Early summer	12.4	< 0.001
	Midsummer	5.4	0.014

Table 3-2.5. Results of one-way ANOVA for differences in decline of density of 2020 cohort among the three populations for each survey period. Significant differences are underlined.

		Decline of density	
Age	Period	*F*	*P*
0+	Midsummer – Spring	7.9	0.002
	Spring – Early summer	3.3	0.055
1+	Early summer – Midsummer	0.4	0.666
	Midsummer – Spring	0.1	0.995
	Spring – Early summer	0.1	0.908
2+	Early summer – Midsummer	1.4	0.254

Table 3-2.6. Results of one-way ANOVA for differences in persistence rate among the three populations for each survey season. Significant differences are underlined.

		Persistence rate	
Age	Season	*F*	*P*
1+	Spring	8.5	< 0.001
	Early summer	1.8	0.179
	Midsummer	0.9	0.428
2+	Spring	1.7	0.203
	Early summer	1.9	0.169
	Midsummer	1.8	0.178

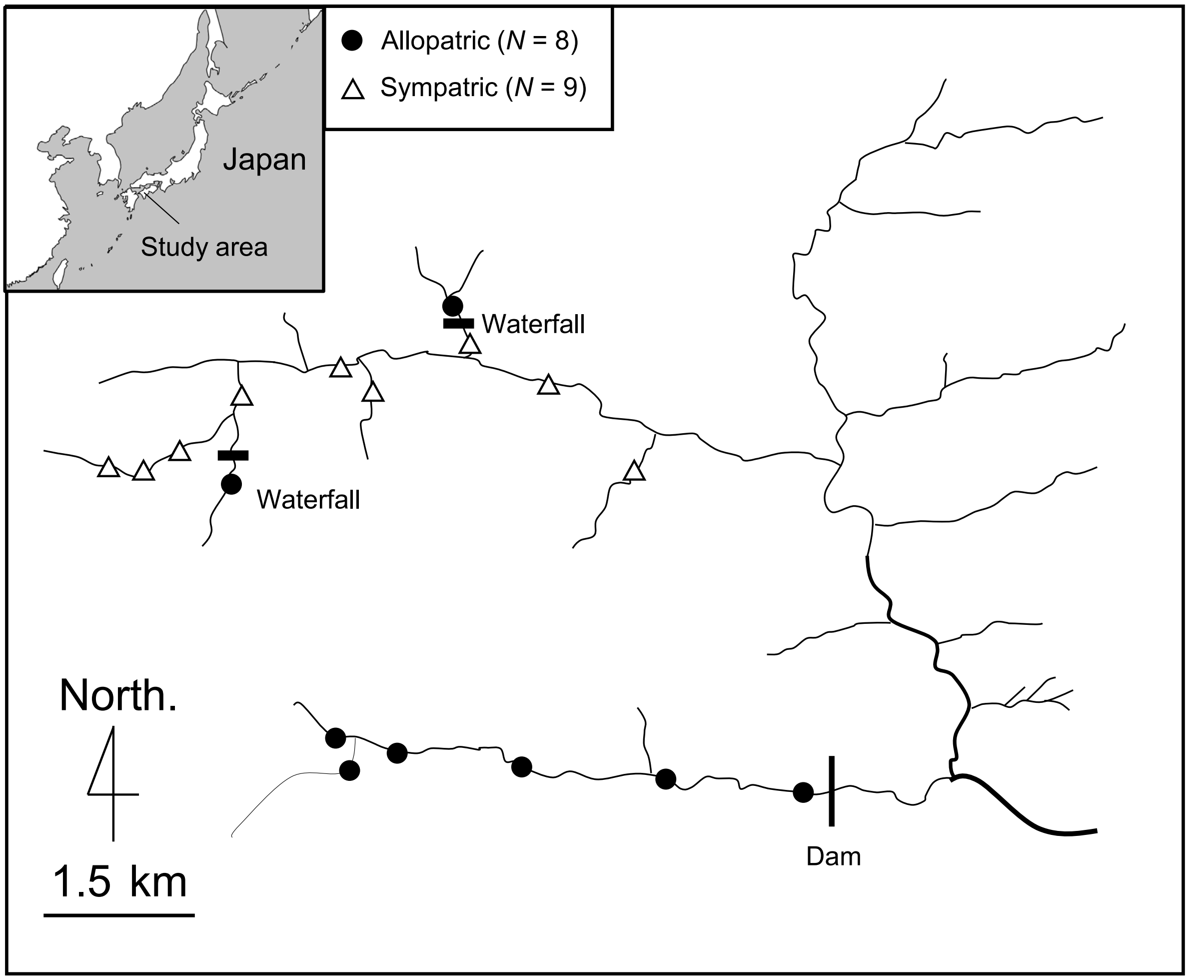

Fig. 3-2.1. Map of the study area in the Kurokawa River, Shikoku, southwestern Japan. Solid circle and open triangle indicate allopatric and sympatric reaches, respectively.

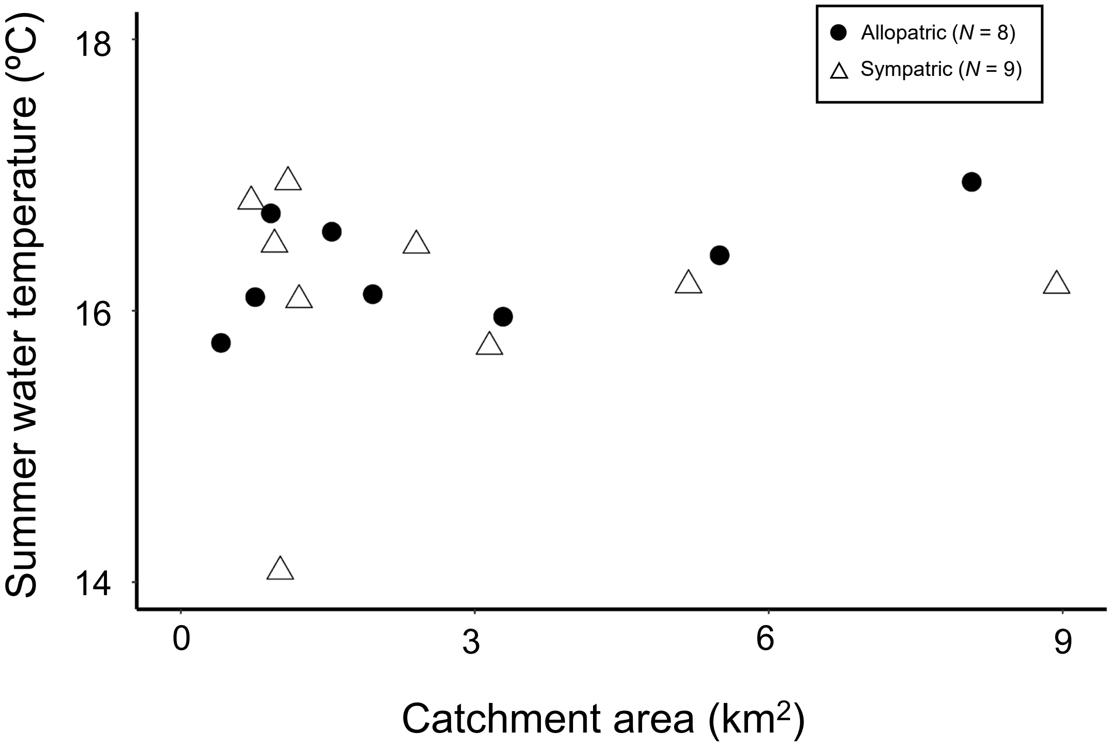

Fig. 3-2.2. Catchment area and summer water temperature of allopatric (solid circle) and sympatric reaches (open triangle)

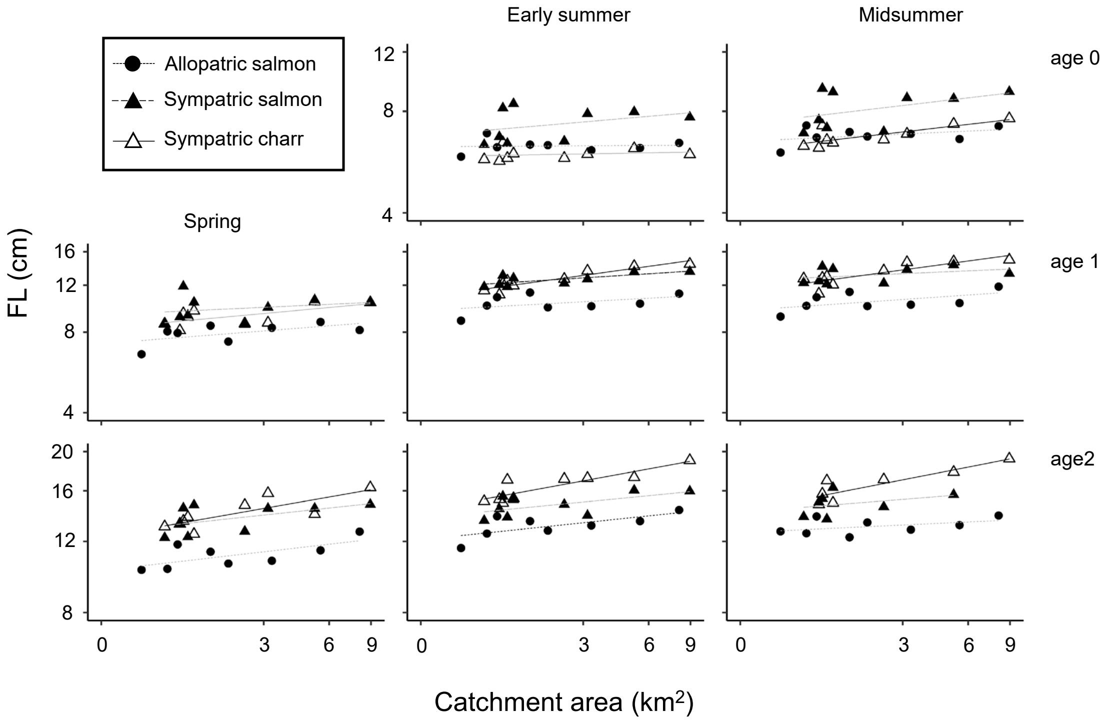

Fig. 3-2.3. Mean FL of 2020 cohort of the three populations in relation to catchment area in each survey season. Solid and open represent red-spotted masu salmon and white-spotted charr, respectively, with circle and triangle indicating allopatric and sympatric reaches, respectively. Black and grey regression lines represent significant and insignificant relationships, respectively.

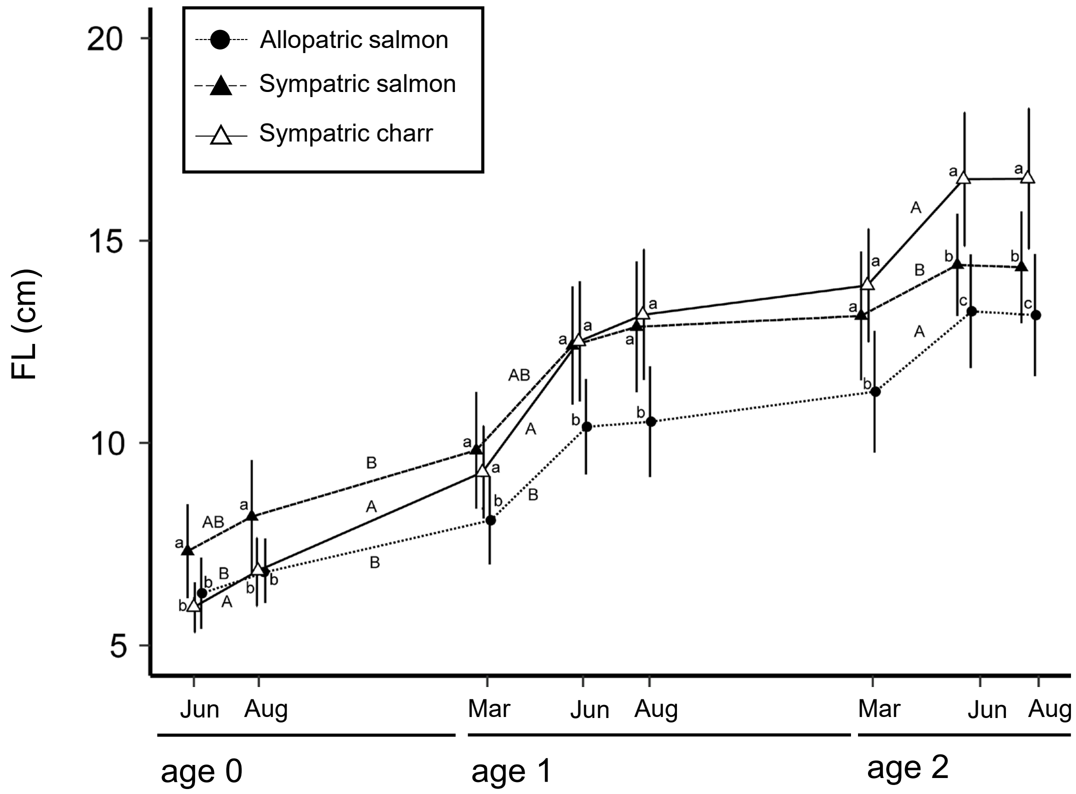

Fig. 3-2.4. Fork length of the three populations, allopatric salmon (solid circle), sympatric salmon (solid triangle) and sympatric charr (open triangle) in each survey season. Symbols (FL) and lines (growth rate) denoted by same letters (a, b and c for FL; A and B for growth rate) are not significantly different by Tukey–HSD test.

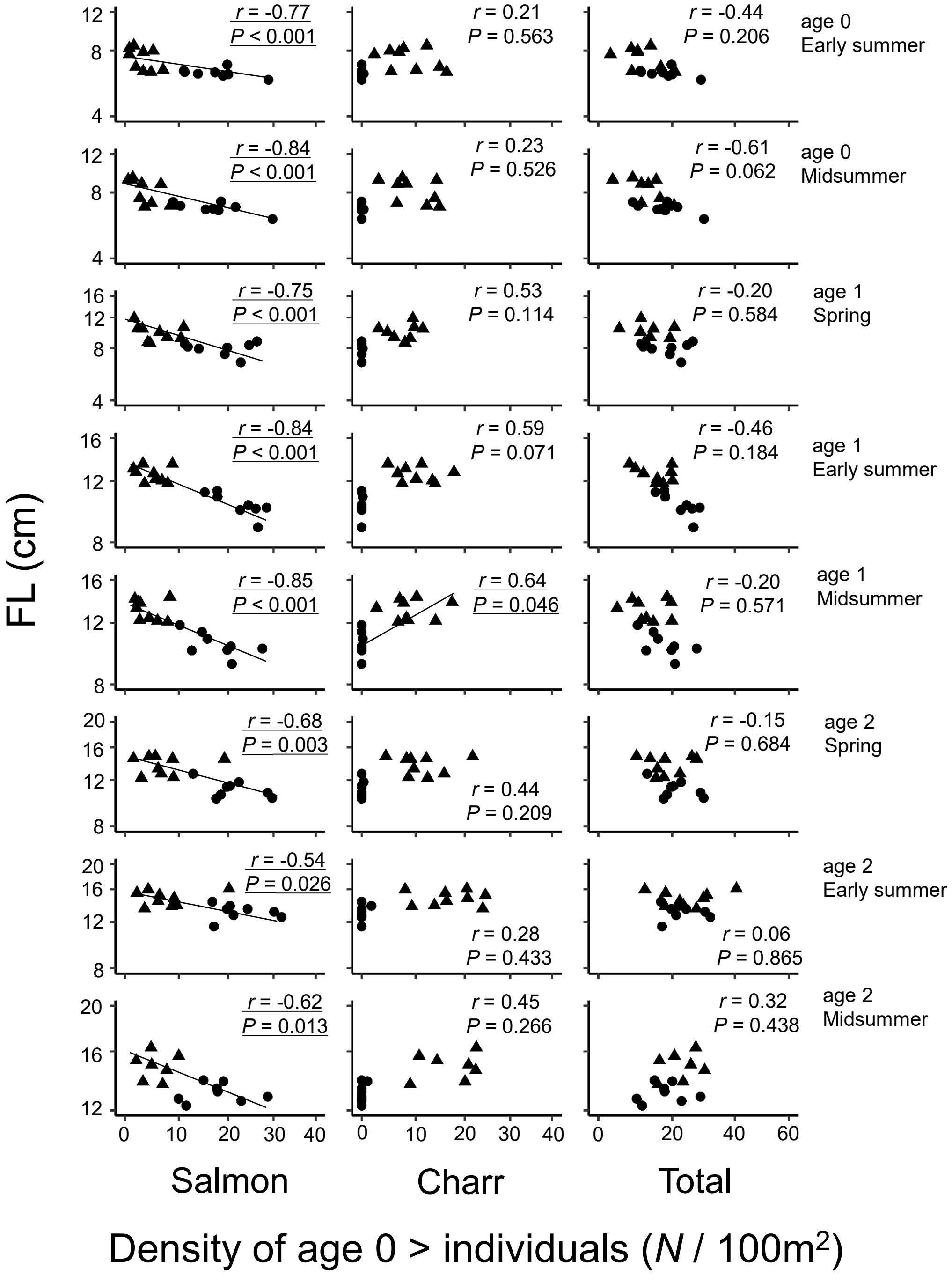

Fig. 3-2.5. Mean FL of 2020 cohort of allopatric (solid circle) and sympatric salmon (solid triangle) in relation to each density for each survey season. Regression lines represent significant correlations.

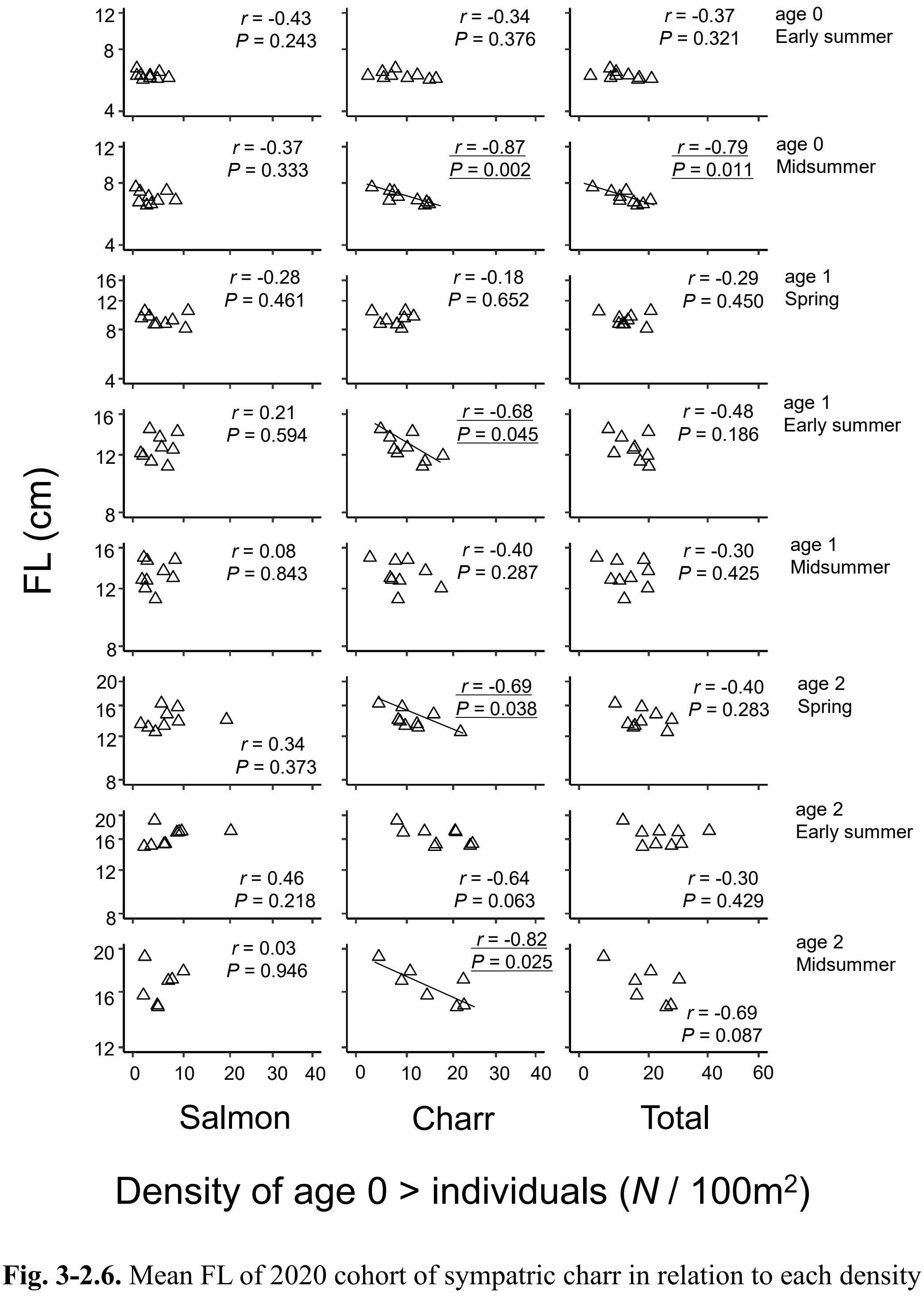

Fig. 3-2.6. Mean FL of 2020 cohort of sympatric charr in relation to each density for each survey season. Regression lines represent significant correlations.

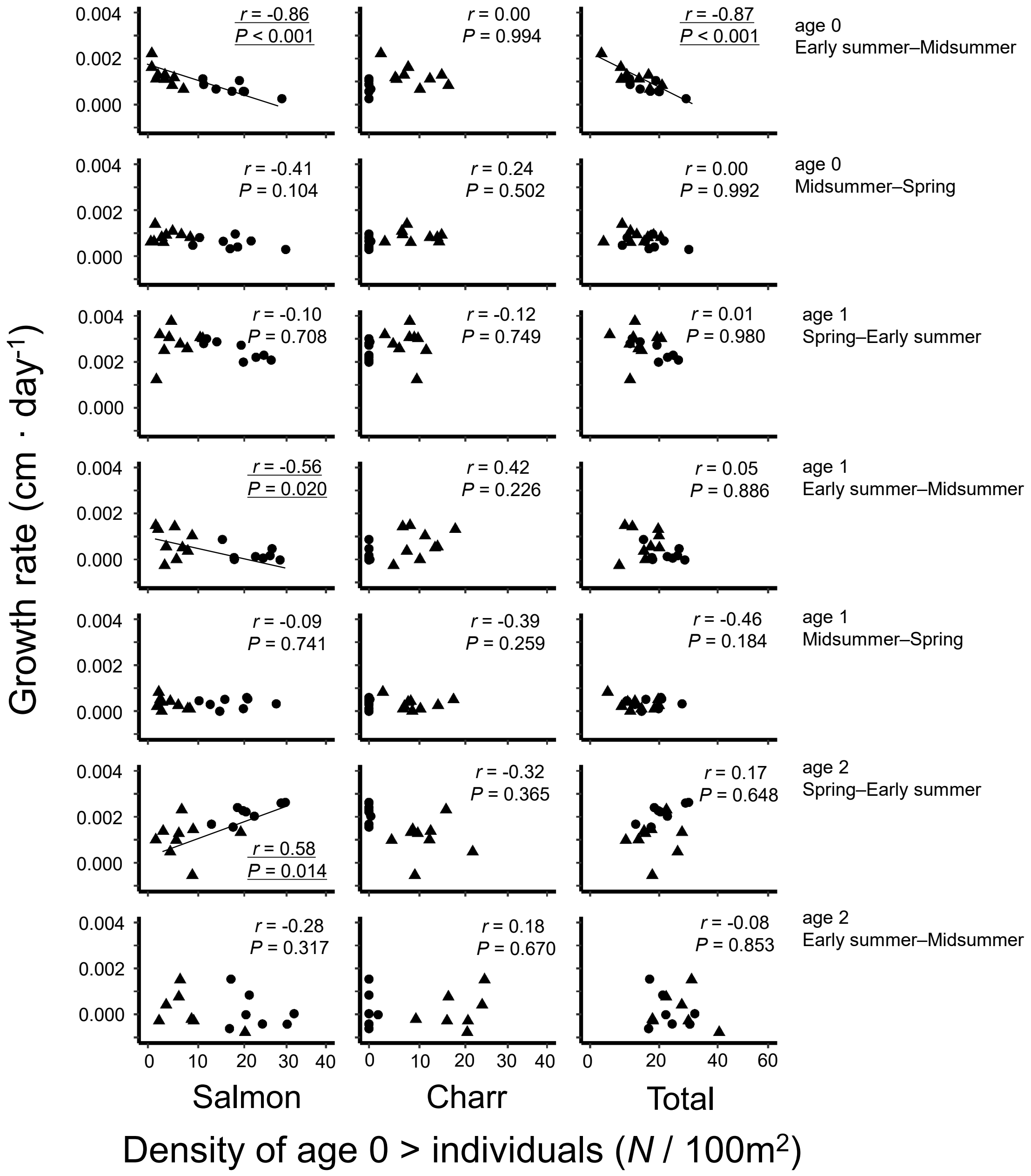

Fig. 3-2.7. Between-season growth rate of 2020 cohort of allopatric (solid circle) and sympatric salmon (solid triangle) in relation to each density for each survey period. Regression lines represent significant correlations.

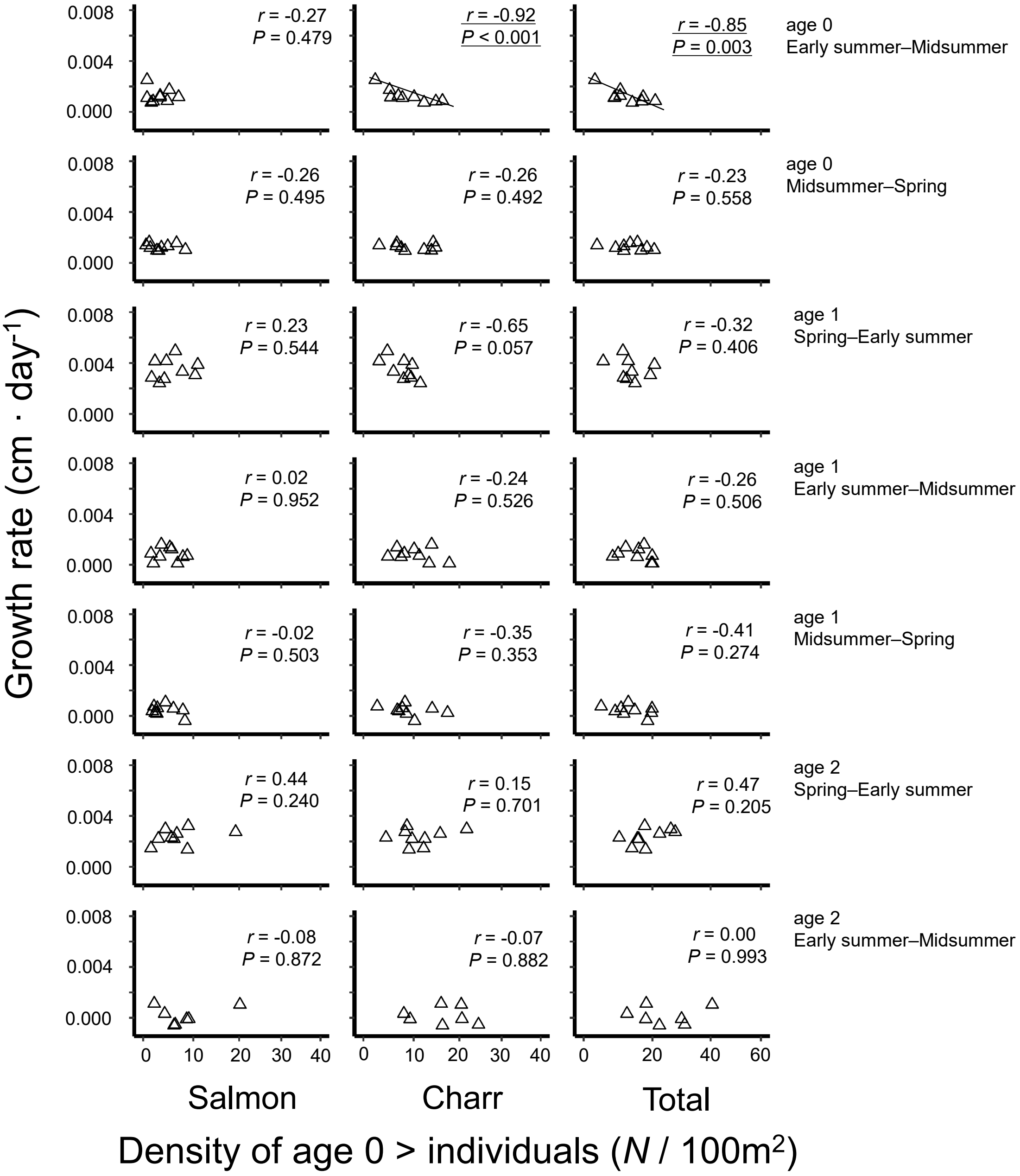

Fig. 3-2.8. Between-season growth rate of 2020 cohort of sympatric charr in relation to each density for each survey period. Regression lines represent significant correlations.

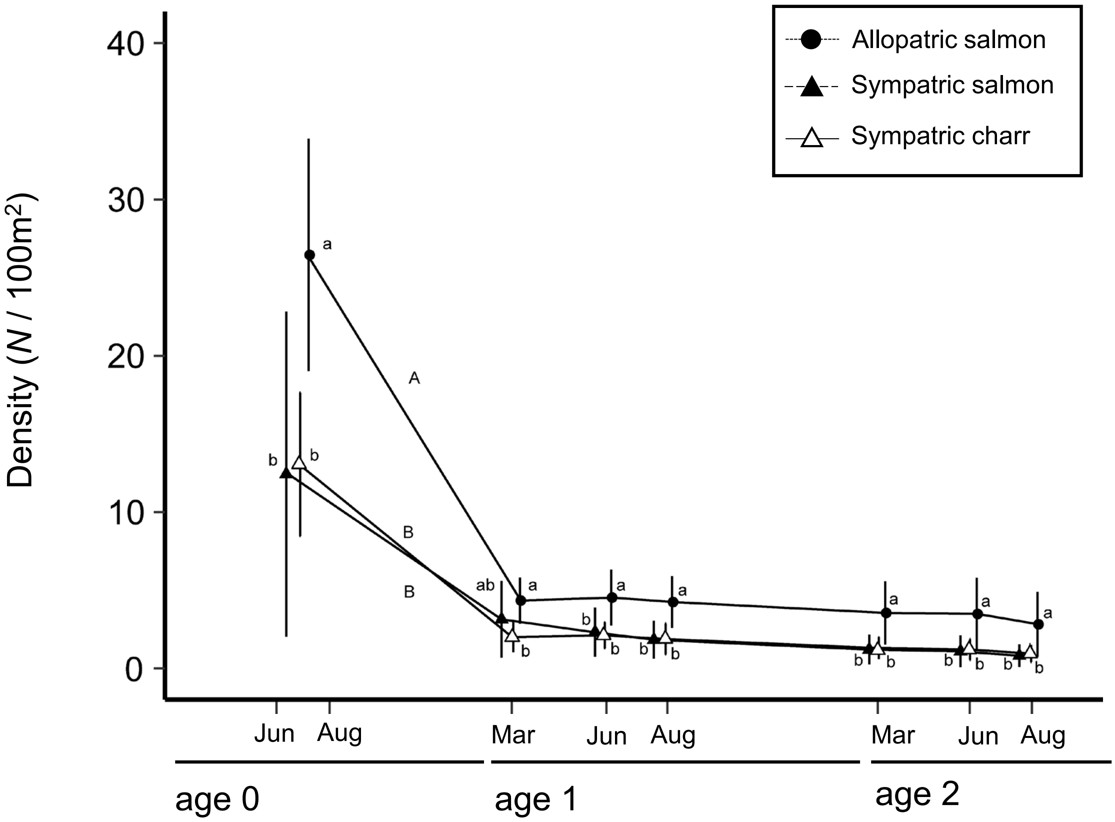

Fig. 3-2.9. Density of 2020 cohort of the three populations, allopatric salmon (solid circle), sympatric salmon (solid triangle) and sympatric charr (open triangle). Symbols (density) and lines (decline of density) denoted by same letters (a and for density; A and B for decline of density) are not significantly different by Tukey–HSD test.

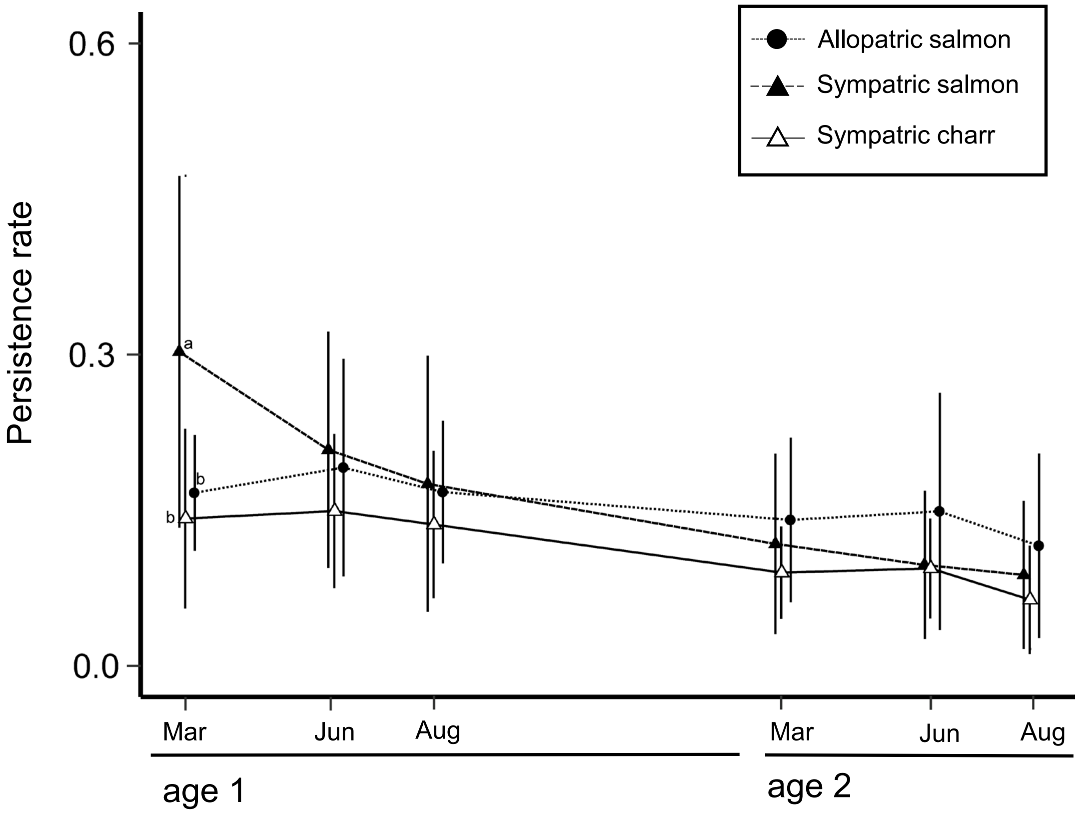

Fig. 3-2.10. Persistence rate of 2020 cohort of the three populations, allopatric salmon (solid circle), sympatric salmon (solid triangle) and sympatric charr (open triangle). Values denoted by same letters are not significantly different by Tukey–HSD test.

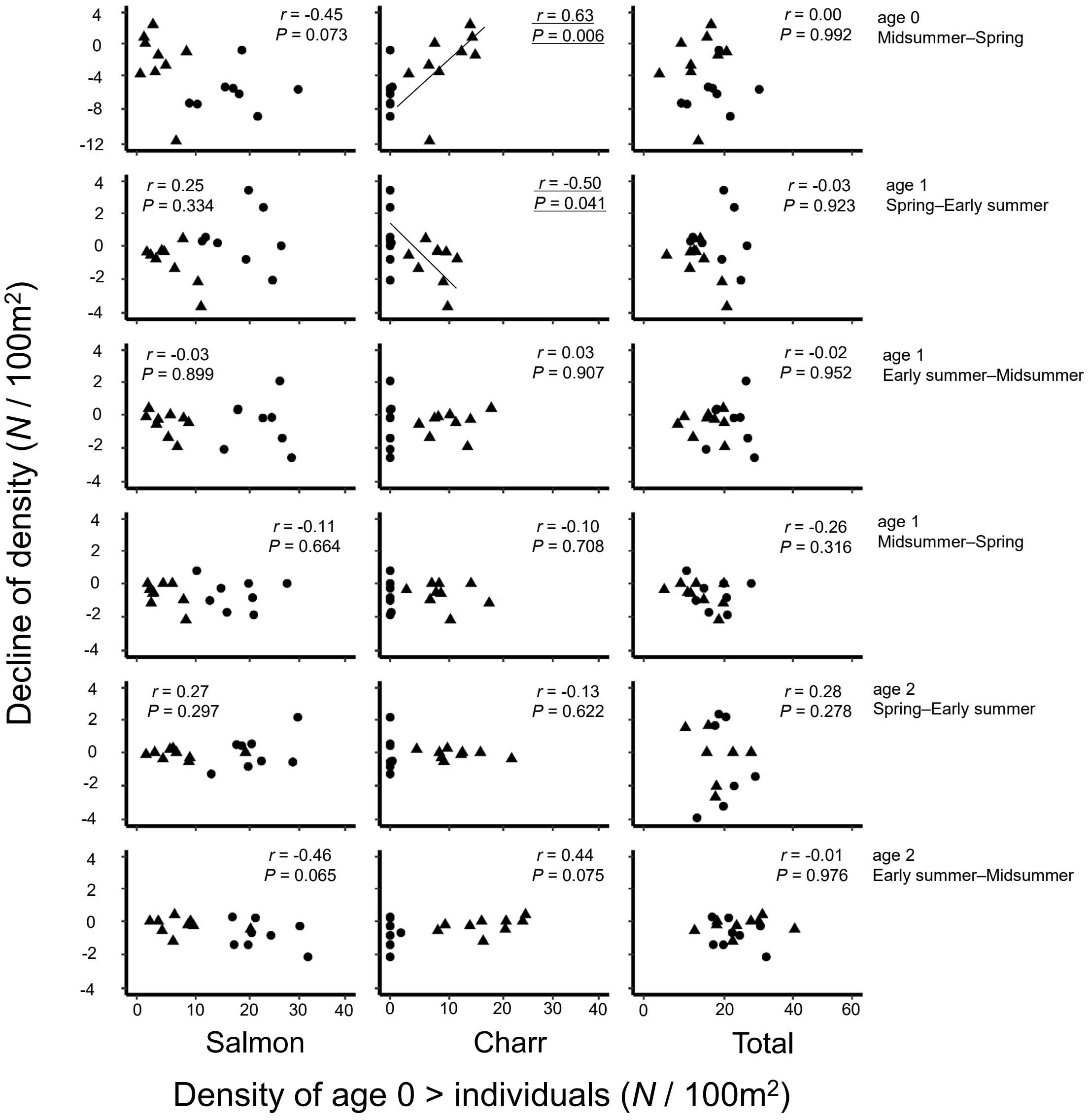

Fig. 3-2.11. Decline of density of 2020 cohort of allopatric salmon (solid circle) and sympatric salmon (solid triangle) in relation to each density for each survey period. Regression lines represent significant correlations.

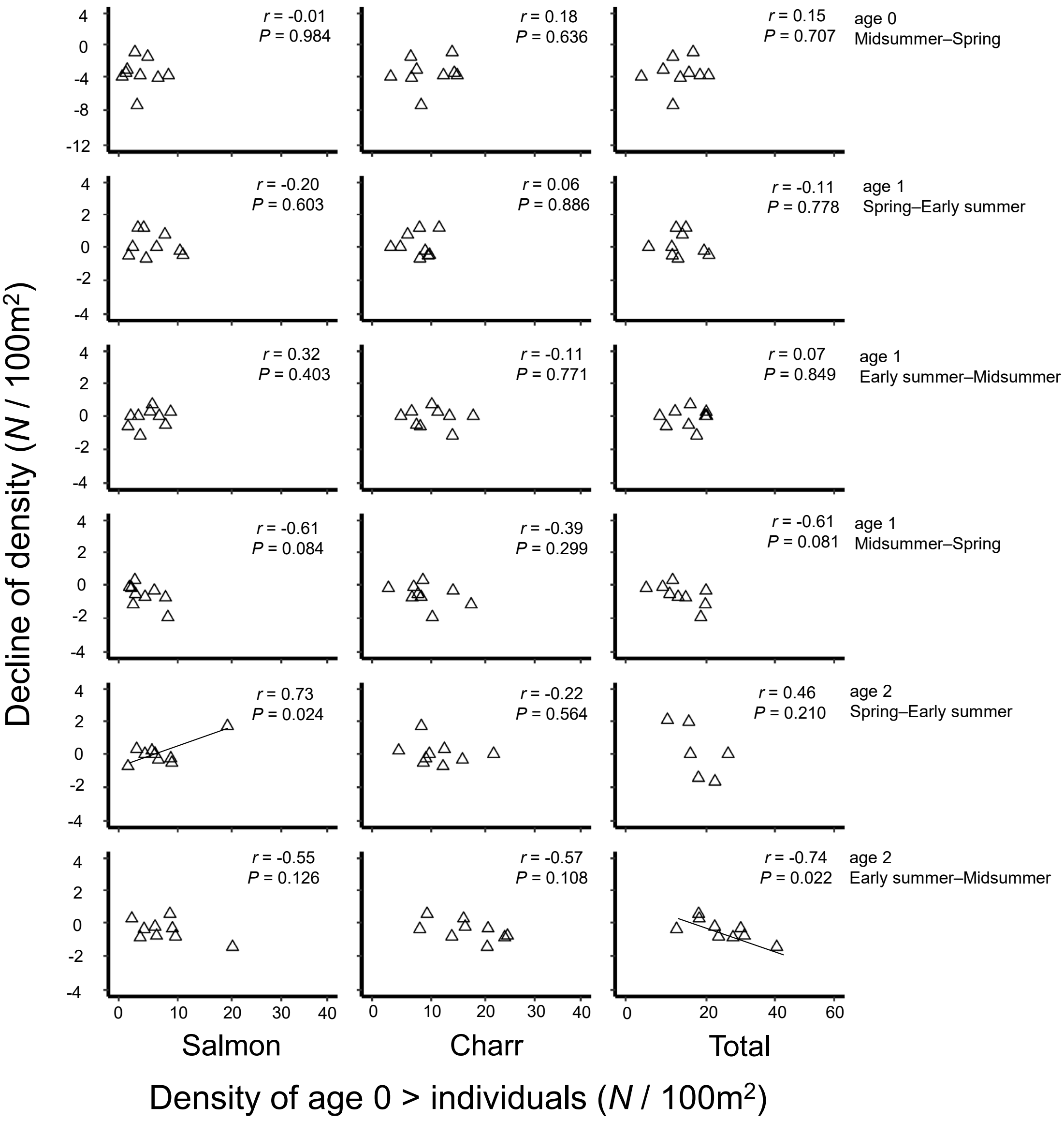

Fig. 3-2.12. Decline of density of 2020 cohort of sympatric charr in relation to each density for each survey period. Regression lines represent significant correlations.

3-3. Conclusion: factors in facilitating species displacement

In this chapter, I examined two potential mechanisms of displacement of native red-spotted masu salmon by introduced white-spotted charr. In chapter 3-1, I showed upstream increase in overlap in spawning-habitat characteristics between the two species, suggesting that redd superimposition can be a potential mechanism of displacement of red-spotted masu salmon in upper reaches. However, redd superimposition could not be actually observed in this study. Therefore, future studies need to examine occurrence and actual effects of redd superimposition by using experimental approaches, such as experimental re-introduction of red-spotted masu salmon in the upper reaches dominated by the non-native white-spotted charr. On the other hand, in chapter 3-2, although no longitudinal reversal of growth between the two species was observed, the three-year monitoring survey revealed that white-spotted charr grew faster and became larger than red-spotted masu salmon at age 2, despite their smaller initial body size. Because competitive superiority of their interference competition for feeding habitat is determined depending on body size (Nakano 1995b), white-spotted charr would become superior to red-spotted masu salmon in interference competition after age 2. Results of chapter 3-2 showed negative effects of white-spotted charr on growth of red-spotted masu salmon in spring at age 2. Furthermore, at age 1, when white-spotted charr caught up in size with red-spotted masu salmon, white-spotted charr negatively affected persistence of red-spotted masu salmon. Thus, high growth of white-spotted charr would be one major factor facilitating the establishment and dominance of the introduced white-spotted charr.

Although my results clearly showed that growth rate of white-spotted charr was higher than that of red-spotted masu salmon, it is questionable whether the higher growth of white-spotted charr than red-spotted masu salmon is a general trend. For example, Nakano (1995b) reported a contrasting finding that growth of masu salmon was higher than white-spotted charr in Honshu Island, central Japan. In his study pool, masu salmon grew larger than white-spotted charr during early summer. Thus, superiority of their growth can change depending on environmental conditions, although I cannot observe longitudinal reversal of their growth in my study area. It is important to clarify factors causing species-specific differences in growth potential between white-spotted charr and masu salmon for better understanding of their interspecific interactions.

Although the superiority of white-spotted charr can be explained by their higher growth, it is unclear how small age-0 individuals of white-spotted charr can grow rapidly under the competitive pressure from native red-spotted masu salmon. One possible factor is the difference in habitat use between the two species. During my field survey, age-0 individuals of white-spotted charr were often observed in woody debris jams, where red-spotted masu salmon were rare. Such habitat partitioning may moderate interference interactions with masu salmon. Detailed investigation of habitat use by the two species during the age 0 stage will be needed.

Most previous studies examined mechanisms of longitudinal replacement of salmonids using experimental approaches (De Staso and Rahel 1994; Taniguchi and Nakano 2000; McHugh and Budy 2005; McMahon et al. 2007). In this chapter, I revealed that superiority of growth and frequency of redd superimposition can be factors replacement of salmonids. Differences in long-term growth across life stage and spawning habitat have rarely been examined as factors affecting longitudinal replacement of salmonids, because it would be difficult to examine these effects by experimental approaches. Consideration of such effects can contribute to better understanding of mechanisms underlying longitudinal replacement of salmonids.

4. Concluding remarks

Processes of fish assemblage organisation can be roughly divided into regional and local processes in metacommunity theory (Leibold et al. 2004). This concept is useful for disentangling complex processes of fish assemblage organisation. In this dissertation, I explored mechanisms of fish assemblage organisation, focusing on fish movement as a regional process in a lowland braided river (chapter 2) and biotic interactions as a local process in headwater streams (chapter 3). This regional-local framework would be useful not only for understanding of mechanisms underlying fish assemblage organisation, but also for conservation strategies. Biodiversity of freshwater fish is threatened (Hermoso et al. 2015; Ishiyama et al. 2016; Schofield et al. 2018; Stoffels et al. 2022), and effective management would be necessary for maintenance of fish assemblages. Uchida and Inoue (2010) pointed out that, for effective management, maintenance of habitat connectivity has priority over improvement of local habitat conditions in areas where effects of regional processes on fish assemblage override those of local processes. Although improvement of local habitat conditions has been widely conducted to conserve fish assemblages, habitat connectivity and arrangement should also be considered for effective conservation. Better understanding of regional and local processes would contribute not only to development of fish ecology, but also to effective management.

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7. Summary

Processes of assemblage organisation in a local habitat are roughly classified into regional and local processes. Both processes are important for all communities and their relative contribution changes depending on characteristics of the target local habitat per se, its connectivity to surrounding habitats and dispersal characteristics of organisms. In river systems, environmental conditions change along the course of streams from headwater to the mouth. Such longitudinal environmental gradients affect the relative importance of regional and local processes in fish assemblage organisation. In general, lowland river systems consist of various habitats, such as main channels, tributaries, ponds, wetlands, paddies and ditches, forming highly complex networks. In such systems, frequent movements of fishes can mask effects of biotic interactions and local habitat conditions on fish assemblages. In contrast to lowland river systems, headwater streams are characterised by small and isolated habitats with low productivity. In such systems, effects of local processes (e.g. biotic interactions) on fish assemblage organisation can override those of regional processes. In this dissertation, I explored mechanisms underlying fish assemblage organisation in a lowland braided river and upper, headwater streams, focusing on regional and local processes, respectively.

Effects of fish movement in lowland freshwater systems

In lowland river systems, I focused on effects of fish movement on assemblage organisation as a regional process. During dispersal or movement through a river network, fish have to select their way at each junction (i.e. the confluence of two channels) in the network, and their channel selection (route selection) would be reflected in the spatial variations in fish assemblage composition. First, I examined channel selection by fish during movement and its effects on local fish assemblage using braided channels. The channel-selection survey showed that fat minnow (*Rhynchocypris oxcycephala*) and spined loach (*Cobitis* sp. BIWAE type A) selected channels with lower flow volume. In pools in the braided channels, strong positive correlations were found between the density of the two species. These results suggest that the fish assemblage composition of local habitats in our braided river reflected channel selection by fish during their movement. Route selection by fish during dispersal or movement can be a notable factor determining the assemblage composition of freshwater fish.

Next, I explored seasonal movement of fishes at a confluence of surface-water and groundwater channels. In braided rivers, networks of groundwater-fed and surface-water dominated channels cause a high variability in stream water temperature in space and time. Fishes in braided channels may exploit such spatiotemporal thermal heterogeneity through seasonal movement. I surveyed seasonal habitat use by fishes at a confluence of groundwater and surface-water channels. The seasonal survey revealed that pale chub (*Opsariichthys platypus*) density was higher in the groundwater channel than in the surface-water channel in winter and vice versa in summer. These spatial variations of pale chub density were related to water temperature both in winter and summer, suggesting their seasonal movement between the two channels to seek better thermal conditions. Thus, groundwater seeps can provide important winter habitats for warmwater fishes and the close proximity of channels having contrasting thermal regimes is an important aspect of braided rivers for persistence of diverse fish assemblages. Overall, the results of these two studies using a braided-channel network suggest the importance of habitat connectivity for maintenance of fish assemblage. This importance found in the braided channels can be applied also to larger networks, such as river-floodplain systems, in lowland rivers.

Interspecific interactions in headwater streams

In headwater streams, I focused on interspecific interactions as a local process in assemblage organisation. In upper reaches of rivers, longitudinal species replacement has often been reported for various pairs of stream salmonids. White-spotted charr (*Salvelinus leucomaenis* subspp.) and masu salmon (*Oncorhynchus masou* subspp.) are common stream salmonids in Japan. In southwestern Japan where white-spotted charr is not originally distributed (i.e. Shikoku and Kyushu), introduced white-spotted charr populations have established in several streams inhabited by native masu salmon. In the Kurokawa River, introduced white-spotted charr has created the common longitudinal pattern (upstream and downstream dominance by white-spotted charr and masu salmon, respectively), by displacing native red-spotted masu salmon in upper reaches. For salmonids, size-dependent dominance hierarchies strongly affect growth and survival of individuals within each local habitat. Because age-0 white-spotted charr is smaller than age-0 red-spotted masu salmon due to late spawning timing, white-spotted charr seems to be inferior to red-spotted masu salmon. However, introduced white-spotted charr has displaced native red-spotted masu salmon in upper reaches, suggesting that white-spotted charr has some advantages to red-spotted masu salmon in upper reaches. I explored mechanisms of displacement of native red-spotted masu salmon by introduced white-spotted charr in upper reaches.

First, I focused on spawning timing, and hypothesised that smaller channels of upper reaches would have higher potential of redd superimposition owing to lower availability of spawning habitat. The high risk of redd superimposition in upper reaches can provide a competitive advantage to late-spawning white-spotted charr and may cause displacement of native red-spotted masu salmon. Spawning-habitat survey showed that 1) the habitat availability decreased upstream as channel size decreased, and 2) characteristics of spawning habitat highly overlapped between the two species in small channels, whereas those differed significantly between the two species in larger channels, suggesting that redd superimposition can be a potential mechanism causing displacement of red-spotted masu salmon in the upper reaches.

Next, I explored differences in growth along streams between the two species. Considering their size-dependent dominance hierarchy, differences in growth can be an important factor affecting their competitive superiority. If white-spotted charr grow faster than red-spotted masu salmon in upper reaches whereas vice versa in lower reaches, this longitudinal reversal of growth can be a cause of displacement of red-spotted masu salmon in upper reaches. I conducted a three-year monitoring survey to examine whether 1) the longitudinal reversal of growth occurs between white-spotted charr and masu salmon, and 2) white-spotted charr negatively affect growth and persistence of red-spotted masu salmon. Although no longitudinal reversal of growth between the two species was observed, my monitoring survey revealed that white-spotted charr grew faster and became larger than red-spotted masu salmon at age 2, despite their smaller initial body size. After age 1, when white-spotted charr caught up in size with red-spotted masu salmon, white-spotted charr negatively affected persistence and growth of red-spotted masu salmon. Thus, high growth of white-spotted charr would be one major factor facilitating the establishment and dominance of its population. Overall, my results suggest that the introduced white-spotted charr in the study area has advantages in growth and spawning habitat use, which could be important factors facilitating the displacement of red-spotted masu salon. These explorations may be applied also to the longitudinal replacement of salmonids in general.