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Freshwater Biology

Spatially variable hydrological and biological processes shape diverse post-flood aquatic communities

Running head: Flood shape diverse aquatic communities

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Keywords

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Abstract

1. Diverse aquatic environments in floodplains support high biodiversity, including plankton, benthos, nekton (fish), and amphibians. Variation in aquatic communities among waterbodies should be explained not only by the spatial variation in the environment at low flow but also by the hydrological dynamics and biological responses over flood and recession periods. However,

very few studies have examined the formation processes of floodplain aquatic communities over flood periods.

2. In this study, we aimed to obtain a mechanistic understanding of the assembly of aquatic communities on a temperate floodplain by conducting intensive fieldwork during and after seasonal flooding. The study was conducted in the Butokamabetsu River watershed in northern Hokkaido, where snowmelt causes annual spring floods. At peak flow, floodwater not only flow through main stream river and the extant side channels, but also flow through some palaeo-side channels, which are usually isolated from the mainstream river and harbour stagnant water. As the floods recede, palaeo-side channels become isolated from the mainstream river and their flow cease, but the timing of the flow cessation varied among palaeo-side channels. We hypothesized that this spatial asynchrony in the timing of flow cessations shapes diverse floodplain aquatic communities. Therefore, we conducted field surveys of four faunal groups (plankton, benthos, nekton (fish), and amphibian) during and after the spring flood in 2019.

3. The post-flood aquatic communities varied spatially, according to the flow at peak flood, the timing of flow cessation, and the flow at low flow. Plankton composition was influenced by the water flow at peak flood, and they were more abundant in waterbodies that were never flushed by floodwaters. Fish composition was also influenced by the water flow at peak flood; in particular, salmonids were more abundant in waterbodies that were hydrologically connected to the main stream at peak flood. The presence of amphibian eggs was influenced by the timing of flow cessation; eggs were laid in waterbodies with stagnant water during breeding season. The benthic composition was influenced by flow at low flow. After the flood had receded, these different distribution patterns of the four biological groups led to gradual variation of aquatic communities among waterbodies on a floodplain.

4. Overall, this study showed that hydrological dynamics during flood recession shapes the post-flood aquatic communities, and the spatial variability in the hydrological dynamics and the different responses of the four faunal groups support diverse aquatic communities on a floodplain. Importance of the natural geomorphological complexities, where paleo-side channels with wide range of hydrological connectivity to the river channel co-occur, as well as the natural hydrological dynamics of snowmelt recession, where the flooding discharge gradually decrease over certain period in spring for floodplain aquatic communities are highlighted.

1 INTRODUCTION

Floodplains are one of the most dynamic landscape ecosystems. Many waterbodies on floodplains are formed by fluvial processes such as channel migration and abandonment. Extant and palaeo-side-channels, a representative waterbody type on floodplains, have diverse degrees of hydrological connectivity to a river's main stream: some are permanently connected to the river, some are connected to the river only at times of high flow, and others are never connected to the river (Amoros & Roux, 1988). In many temperate floodplains, spring snowmelt causes long-lasting floods that seasonally expand and gradually contract river channels, thus supporting spatially and temporally dynamic aquatic habitats for various faunal groups, including plankton, benthos, nekton (fish), and amphibians (Tockner, Malard & Ward, 2000).

Although an increasing number of studies have investigated floodplain ecosystems at low flow, few have addressed the spatial and temporal dynamism of floodplain ecosystems during periods of flood (Amoros & Bornette, 2002; Hauer et al., 2016). Studies conducted at low flow have shown that the composition of aquatic communities on a floodplain varies among waterbodies (Tockner et al., 2000; Amoros & Bornette, 2002), and this variation is often attributed to differences in hydrological connectivity to the river. However, most of the floodplains are isolated from river mainstream at low flow when most studies are conducted, and the concept of the connectivity is not well defined. In fact, aquatic communities in floodplain waterbodies are not only influenced by the environmental variation that is observed at low flow; they are also strongly influenced by the hydrological and biological processes during flood and flood recession periods (Thomaz, Bini & Bozelli., 2007; Larsen et al., 2019). For example, flow pulses may differently modify the physical and chemical environment of each waterbody, thereby altering the suitability of habitats for aquatic organisms over time and space (Ward, Tockner & Schiemer, 1999; Tockner et al., 2000). Isolation of aquatic organisms from the river limits their dispersal and migration and thus constrains their distributions (Ward et al., 1999; Crook et al., 2020). Geomorphological and hydrological characteristics may also influence breeding site selection by amphibious organisms such as frogs (Kupferberg, 1996) and aquatic insects (Encalada & Peckarsky, 2006). Therefore, to gain a mechanistic understanding of aquatic community assembly on a floodplain, it is necessary to closely examine the spatial and temporal components of the hydrological dynamics over flood periods and investigate the respective responses of diverse faunal groups.

Different responses of different faunal groups to the hydrological dynamics over flood periods may drive the diversity of aquatic communities in floodplain waterbodies. In floodplain waterbodies, we observe at least four biological groups, namely, plankton, benthos, nekton (fish), and amphibians, whose responses to the hydrological dynamics should differ according to their ecological characteristics. For example, limitations to dispersal and migration may be critical for mobile organisms such as fish (Bolland et al., 2012; Crook et al., 2020). Flow pulses during flood periods may have a large influence on plankton, which might be flushed downstream by floodwaters (Van den Brink, Van Katwijk & Van der Velde, 1994), and on benthos, through mobilization of substrate materials (Arscott, Tockner & Ward, 2005). A growing number of studies have addressed the use of floodplain habitats by different taxonomic or faunal groups (Van den Brink et al., 1994; Morand & Joly, 1995; Bolland et al., 2012; Gallardo et al., 2014), but only a few studies have simultaneously examined the distributions of the distinct faunal groups that inhabit a river-floodplain system (Tockner, Schiemer & Ward, 1998). However, given that hydrological dynamics influences each faunal group differently, by focusing on a single faunal group, the critical environmental gradient that is required to support diverse aquatic communities may be underestimated. Variation in responses to hydrological dynamics among faunal groups is one factor that supports diverse aquatic communities on a floodplain, and gradients that include a wider range of hydrological environments may support more diverse aquatic communities.

In this study, we aimed to obtain a mechanistic understanding of the assembly of aquatic communities on a floodplain that would enable us to predict the distribution of aquatic biota on a floodplain from the hydrological dynamics. We hypothesized that spatial asynchrony in flow cessations associated with side channel isolation from the main stream during flood recession shapes diverse floodplain aquatic communities, which is driven by the differential responses of various faunal groups to the hydrological dynamics. First, to examine the link between hydrological dynamics and biological responses, we collected biological data at multiple times during the flood recession period from four selected waterbodies with different hydrological connectivity to the river over the flood recession period (hereafter, the flood-recession survey). Second, we evaluated the residency of fish in palaeo-side channels by using an isoscape approach, because some fish may be mobile whereas other faunal groups unlikely move between sites. Finally, after the flood had receded, we surveyed aquatic communities in 26 waterbodies where we had recorded different hydrological patterns over the flood recession period (hereafter, the post-flood survey). Considering the results of both surveys, we examined how the hydrological dynamics of snowmelt recession shaped the post-flood aquatic community and showed how a range of hydrological connectivity to the river supported co-existing diverse aquatic communities on a floodplain.

2 METHODS

2.1 Study system

The study was conducted on the Butokamabetsu River floodplain, located in the Hokkaido University Uryu Experimental Forest, northern Japan (44°24’N, 142°07’E) (Fig. 1). The floodplain is covered predominantly by 1–2 m high broad-leaf bamboo (*Sasa senanensis*) and a sporadic mix of deciduous trees such as alder (*Alnus japonica*) and Japanese white birch (*Betula platyphylla*). Some wetlands and some areas of humic soils are distributed on the floodplain (Shibata et al., 2004; Ogawa et al., 2006). The main stream of the Butokamabetsu River, which is about 10 m wide under summertime low-flow conditions, has many extant and palaeo-side channels. Extant side channels remain connected to the main stream even during periods of low flow and the water remains flowing all year around. Palaeo-side channels are old side channels that have become isolated from the main stream through the loss of their upstream connection with the river as a result of fluvial sediment and debris accumulation and flood dynamics. Many palaeo-side channels, including our study sites, harbour stagnant water during low flow (also called oxbow lakes). Floodwater flows into some of the palaeo-side channels at high flow, and the water keeps flowing through palaeo-side channels until the river water level drops to certain levels for respective paleo-side channel depending on their geomorphology. Therefore, a gradient of hydrological connectivity to the river exists among waterbodies on the floodplain: extant side channels, seasonally connected palaeo-side channels, and permanently isolated palaeo-side channels.

The study area receives mean annual precipitation of 1236 mm, largely as snow, and snow cover usually lasts from late November to early May, with a maximum depth of ~3 m (Aoyama et al., 2011). Snowmelt typically occurs from April to May, and the river discharge is elevated over this period (Fig. 2). Amphibians, including the Ezo brown frog (*Rana pirica*) and the Ezo salamander (*Hynobius retardatus*), breed and their larvae mature during the snowmelt period on the floodplain. Fish fry of various species develop in the floodplain waterbodies. We conducted a field study in 2019 from the peak of the snowmelt season through the flood recession to the low-flow period (10 May to 17 June).

2.2 Flood-recession survey

We conducted a flood-recession survey to characterize the temporal dynamics of hydrology and water chemistry, as well as the biological responses of the four faunal groups to the environmental changes as floodwater receded. As focal study sites for the flood-recession survey, we selected four representative waterbodies with different degrees of connectivity to the mainstream river (Fig. 2): “No flow” sites A and B, a “Early” site C, and a “Late” site D, as determined during the post-flood survey (see section 2.4). At these four focal sites and at one mainstream site (site E), we recorded environmental data approximately every five days from 14 May through 17 June 2019. At each site, we measured pH and conductivity with a portable pH/COND meter (D-74, HORIBA, Kyoto, Japan) and dissolved oxygen and water temperature with a portable multimeter (HQ-30d, HACH, Loveland, Colorado, USA). We collected a 200-ml water sample in prewashed polyethylene bottles for nutrient analysis. Water samples were filtered through a GF/F filter within 24 h, and both the GF/F filter and the filtered water were frozen for later chlorophyll-*a* analysis (as an indicator of phytoplankton density) and nutrient analysis in the laboratory. Furthermore, 20 L of water was filtered through a 70-µm-mesh plankton net and preserved in Lugol solution for zooplankton analysis.

To examine the distributional shift of fish from the peak flooding season to the end of the flood, we conducted fish surveys on 22 May and 12 June 2019. Fish were captured with a backpack electrofishing unit (Model LR-24, Smith-Root Inc., Vancouver, Washington, USA) using a pulsed direct current setting (300–400V, 30-45Hz, and 25% duty cycle). A crew of three or four study participants sampled in an upstream direction. The entire area of small waterbodies or the first 20–120 m of palaeo-side channels at the site longer than 120 m were sampled by the single-pass method. All fish collected in the survey on 22 May were identified to species and released back to the same site alive, but some individuals collected on 12 June were sacrificed for the stable isotope analysis (described below). The fish catch per unit effort was calculated by dividing the fish count by the total habitat area sampled.

To examine the timing of amphibian breeding, we recorded the presence/absence of amphibian eggs by species on 15 and 29 May and 11 June 2019. This survey was conducted at all 26 sites, including the four focal sites, where the post-flood survey was conducted (see section 2.4).

2.3 Isoscape analysis of the stable carbon isotope ratio

To infer the residency of fish within each palaeo-channel, we conducted a spatial analysis of stable carbon isotopes (isoscape analysis: see Bowen, 2010) in fishes and benthic invertebrates, which are the main prey of the fishes. We focused on the natural spatial variation of stable carbon isotope ratios among the waterbodies, which in anoxic ponds reflects the contribution of methane-derived carbon (Kohzu et al., 2004). The stable carbon isotope ratio of consumer species reflect that of their diet (DeNiro & Epstein 1978). Therefore, fish carbon isotope ratios should reflect the carbon isotope ratios of items that they had consumed some days before they were captured; the duration of the prey signals reflected in the fish tissue can vary from a few days to a few weeks, depending on the fish species and conditions and environmental factors (Weidel et al., 2011). Therefore, the stable carbon isotope ratios of fish that have inhabited a local waterbody for a few weeks before the sampling date should match those of their local prey (i.e., benthic macroinvertebrates). In contrast, the stable carbon isotope ratios fish that have moved between waterbodies with different environments should be more spatially homogeneous than those of their prey items. Further, if only some fish have moved between waterbodies, then stable carbon isotope ratios should exhibit large variation among individuals.

We collected fish and their potential prey items at the four focal sites at the end of the recession period. We collected representative benthic invertebrates with dip nets on 17 June 2019. At each site, we collected 7 to 13 individuals belonging to 12 taxa. We collected most fish samples during the second fish survey on 12 June 2019 (see section 2.2). We collected two supplementary fish samples from site B on 19 June 2020, together with benthic macroinvertebrate specimens. We confirmed that the stable carbon and nitrogen isotope ratios did not differ significantly between sampling years; thus, we pooled the data from 2019 and 2020 for the isoscape analysis. We collected 2 to 10 individuals of the dominant fish species at each site for stable isotope analysis. All fish and benthic invertebrate samples were immediately frozen and transported to Kyoto University for later analysis.

2.4 Post-flood Survey

To examine how the biological responses during the flood, observed in the flood-recession survey, shaped the spatial distribution of the aquatic biota at low flow (post-flood), we conducted a post-flood survey of waterbodies on 12–13 June 2019, after snowmelt had ceased. A total of 26 waterbodies (including both palaeo- and extant side channels) with different degrees of connectivity to the main stream in five spatial blocks along a 10-km segment of the Butokamabetsu River were selected (Fig. 1). We confirmed that there was no significant bias in the distribution of connectivity among the blocks (one-way analysis of variance [ANOVA]; $P = 0.95$). Before the post-flood survey, during and after the flood recession from early May to mid-June, we visited each site every five days to record its connectivity to the river's main stream. During these visits, we visually examined the surface water connection to the main stream at both the upstream and downstream ends of each waterbody. When there were surface water connection upstream, mainstream river water flew-in from the upstream end, flew through the waterbodies, and flew-out from the downstream end. Therefore, in all cases when we observed upstream connection in this study, we also observed downstream connection, and the waterbodies were flushed by flow. In contrast, downstream connection did not make as much influence on the physical environment of the entire waterbodies as the upstream connection. Yet, we assumed the downstream connection could enable the immigration and emigration of fishes. Based on these observations, we categorized the study sites into six connectivity categories (Figs. 1, 2). "Isolated" sites were never connected to the river, even at peak discharge. "No flow" sites were never flushed by floodwaters, because the upstream end of the palaeo-side channel was always closed, but at flood peak they were hydrologically connected to the main stream at their downstream end. At the "Early", "Middle", and "Late" sites, each waterbody was flushed by flow at peak discharge and isolated from the main stream at low flow, but differed by the timing of flow cessation. At "Early", "Middle", and "Late" sites, flow cessation occurred on 23 May, 28 May, and 6 June 2019, respectively. At “Flowing” sites, flow was continuous throughout the study period. Among the 26 sites, 2 were categorized as “Isolated”, 7 as “No flow”, 6 as “Early”, 4 as “Middle”, 3 as “Late”, and 4 as “Flowing” sites.

In the post-flood survey, in addition to measuring the water chemistry, we surveyed four faunal groups: plankton, benthos, nekton (fishes), and amphibians. Water chemistry measurements and water, plankton, and fish sampling were conducted following the same methods as for the flood-recession survey. Benthic invertebrates were sampled with core samplers (13 cm diameter; five times) at most sites, but at 12 sites where the substrate materials were larger than the core size, Surber net samplers (30 cm × 30 cm) were used, and two samples were collected at each site on each sampling date and combined. Benthic samples were immediately sieved through a 0.5 mm mesh and preserved in 99% ethanol for later sorting. Fish were sampled by the same method as for the flood-recession survey, and the presence or absence of amphibian eggs or larvae was also recorded during the post-flood survey.

2.5 Laboratory analysis

All analyses were conducted at the Center for Ecological Research, Kyoto University, Otsu, Japan. Nitrate (NO_3^-) nitrogen was quantified by first reducing nitrate to nitrite using a cadmium coil followed by diazotization with sulfanilamide and coupling with *N*-(1-naphthyl) ethylenediamine dihydrochloride. Ammonium (NH_4^+) nitrogen was quantified by the indophenol blue method. Soluble reactive phosphorous (SRP) was quantified by the molybdenum blue method. A continuous flow auto-analyser (QuAAtro 2-HR, BLTEC, Osaka, Japan) was used for these analyses.

Chlorophyll-*a* was extracted with dimethylformamide, and the mean chlorophyll-*a* content per unit of water was measured by spectro-fluorometry (RF-5300PC, Shimadzu, Kyoto, Japan). Zooplankton individuals > 0.5 mm in size were counted at the sub-order level, and their density per water volume was estimated. Benthic macroinvertebrates were identified to family, and the density of each family per unit area was estimated.

Stable carbon and nitrogen isotope analyses were also conducted at the Center for Ecological Research, Kyoto University. Benthic insect samples were freeze-dried, and their whole bodies were individually ground prior to the analysis. For fish samples, a sample of muscle tissue was dissected out, then freeze-dried and ground for the analysis. A subsample of fish muscle tissues was immersed in chloroform/methanol (2:1) solution for 24 h and then rinsed with methanol to remove lipids. Stable nitrogen isotope ratios of samples without lipid removal and stable carbon isotope ratios of samples after lipid removal were used as the representative values of fish muscle, as described by Sotiropoulos, Tonn & Wassenaar (2004). Stable carbon and nitrogen isotopes were measured with an elemental analyzer/isotope ratio mass spectrometer (EA/IRMS; DELTA-V plus, Thermo Fisher Scientific, United States).. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios are expressed as the per mil (‰). δ^{13}C and δ^{15}N of standard samples and the analytical methods described above were referenced from Tayasu et al. (2011).

2.6 Data analysis

To examine spatial and temporal variations in water chemistry, we conducted a principal component analysis (PCA) of pH, conductivity, DO, NO_3^-, NH_4^+ and SRP data collected at all sites in all seasons. To examine the spatial variation in water chemistry during the post-flood survey, scores on the first PCA axis (PCA1) were compared with the connectivity of each site, where spatial block was included as a random factor in a linear mixed model, by using the lmer function in the lme4 package (Bates et al., 2021) and the anova function in the lmerTest package (Kuznetsova et al. 2020) in the R software environment (R Core Team, 2018). To examine differences in the temporal variation in water chemistry at among the four focal sites with different degrees of connectivity to the main stream, we compared the PCA1 score of the focal sites with the Julian date by one-way ANOVA, including sampling site as a random factor. Additionally, the same analyses were conducted for pH, conductivity, DO, NO_3^-, NH_4^+, and SRP, as well as chlorophyll *a* and zooplankton density. To compare the temporal shift in fish species composition from the peak flood to the end of the flood season and the spatial variation of fish species composition across waterbodies, we performed permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the vegan package (Oksanen et al., 2020). Plankton and fish density data were log-transformed prior to all analysis.

Mean δ^{13}C of benthic macroinvertebrates and fish were estimated at each site. The relationship between hydrological connectivity and the mean δ^{13}C of benthic macroinvertebrates was examined by Spearman's rank correlation test. We conducted a regression analysis between the mean δ^{13}C of benthic macroinvertebrates and the mean δ^{13}C of fish at five sites.

Using the post-flood survey data, we examined how the temporal hydrological dynamics influenced each faunal group by comparing the density and diversity (taxonomic richness) of each faunal group with the hydrological changes over time at each site. We fit five linear mixed models to the data assuming five different distribution threshold (Fig. 2c), and compared their goodness of fit based on their Akaike information criterion (AIC) values. All models included a connectivity factor, described below, and habitat area as fixed effects, and block as a random effect, to control for inherent longitudinal habitat heterogeneity. The first model assumed a hydrological connection at flood peak (river connection on 15 May) influenced the biota, and included as binary factors Isolated sites versus all other sites. The second model assumed that the presence of flow at peak flood (on 15 May) influenced the biota, and included the binary factors Isolated+No_flow sites versus other sites. The third and fourth models assumed that the timing of the flow cessation at each site influenced the biota. The third model assumed that the presence of flow on 23 May influenced the biota and included Isolated+No_flow+Early sites versus Middle+Late+Flowing sites as binary factors. The fourth model assumed that the presence of flow on 28 May influenced the biota, and included Isolated+No_flow+Early+Middle" sites versus Late+Flowing sites as binary factor. The final model assumed that the aquatic communities were structured primarily by the flow at the time of sampling, and included Flowing sites versus all other sites as binary factors. We fit these five models to the data on the total density of each respective faunal group and calculated the AIC value of each model. We then selected the model with the lowest AIC value as the best model for that faunal group. We analysed the diversity (taxonomic richness) of the four faunal groups similarly.

We used multivariate techniques to examine the influence of hydrological connectivity on the aquatic community, including the four faunal groups. Density data of all faunal groups were standardized by using the decostand function in the vegan package (Oksanen et al., 2020) in R prior to analysis. Then we analysed the data of all faunal groups by nonmetric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity index as pairwise beta-diversity values. We applied PERMANOVA procedures to the β-diversity values to test for statistical differences in the biota along the connectivity gradient. To account for spatial patterns, we included "block" as a random effect in this analysis. Finally, we applied a similarity percentage analysis (SIMPER) to examine the contribution of each taxon to the differences in the whole biota. The contribution of each faunal group was inferred by summing the contributions of all taxa belonging to each faunal group.

3 RESULTS

3.1 Physical environment

The all 26 studied waterbodies ranged in width from 0.7 m to 2.9 m, in length from 4.7 m to 160 m, and in depth from 0.08 m to 0.54 m at the time of the post-flood survey (i.e., after the snowmelt flooding). Bottom sediment composition differed among the waterbodies depending on connectivity to the main stream; more connected sites had a lower proportion of organic sediments and contained larger rocks. Width, depth, and water velocity at the four focal sites gradually decreased as the river discharge decreased over the study period.

3.2 Water chemistry

The multivariate analysis of the water chemistry data collected during flood-recession and post-flood surveys revealed a link between the spatial and temporal water chemistry patterns. PCA1 explained 42% of the total variation in the chemistry data (Fig. 3) and was inferred to represent temporal changes in habitat characteristics (ANOVA, $F_{1,29} = 70.3$, $P < 0.05$). Sites with different degrees of connectivity were arranged along PCA1 such that more isolated sites exhibited lower scores (ANOVA, $F_{5,13.5} = 4.6$, $P < 0.05$). Over the course of the flood-recession survey, conductivity and NH_4^+ increased, and pH, DO, and NO_3^- decreased, but temporal changes in SRP were not significant. The spatial data showed that pH and DO were lower at more isolated sites, but connectivity was not significantly related to conductivity, NO_3^-, NH_4^+, or SRP.

3.3 Flood-recession survey

Quantities of both phytoplankton and zooplankton increased as the flood receded (Fig. 3). Chlorophyll-*a*, an indicator of phytoplankton density, significantly increased as the flood receded (ANOVA, $F_{1,23} = 8.16$, $P < 0.05$). During the flood-recession zooplankton survey, a total of 3407 copepods, 47 other crustaceans, and 105 mosquito larvae were counted. Total zooplankton density also increased significantly as the flood receded (ANOVA, $F_{1,23} = 4.38$, $P < 0.05$).

In the fish survey, a total of 89 and 159 individuals were collected on 22 May and on 12 June 2019, respectively, at the four focal sites (Fig. 4). Young-of-the-year charr and trout were recruited to the sampling sites over time; they were found only on the 12 June survey and only at sites C and D, where flow had occurred at peak discharge but had ceased by 6 June. Overall, fish species composition at the four sites did not differ significantly from before to after the flood, and variation in fish species among sites persisted. The PERMANOVA analysis showed that the spatial variation was greater than the temporal variation; the temporal change in fish species composition was not statistically significant (Table S1).

No amphibian eggs were found on 15 May 2019. On 29 May, among the 26 sites, *Rana pirica* eggs were found at 18 sites and *Hynobius retardatus* eggs were found at 14 sites. No additional amphibian eggs were laid between 29 May and 11 June.

3.4 Stable carbon isoscape

δ^{13}C values of benthic macroinvertebrates and fish varied among the sites (Fig. 5; Fig. S1). δ^{13}C values of benthic macroinvertebrates were lower at sites with low connectivity (Spearman's rank correlation test; $P < 0.05$, $\rho = 1$). At the No flow sites A and B, they ranged from –42‰ to –33‰ and from –43‰ to –33‰, respectively, and at sites C (Middle) and D (Late), they ranged from –35‰ to –31‰ and from –31‰ to –27‰, respectively; at site E (on the main stream), they ranged from –30‰ to –25‰. δ^{13}C values of fish were positively correlated with those of benthic macroinvertebrates at each site ($Y = 0.81x - 1.86$, $R^2 = 0.95$, $P < 0.01$). They ranged from –36‰ to –32‰ at site A, from –34‰ to –29‰ at site B, from –39‰ to –25‰ at site C, from –25‰ to –24‰ at site D, and from –25‰ to –25‰ at the site E.

3.5 Post-flood survey

A total of 4626 copepods, 129 other crustaceans, and 350 mosquito larvae (Culicidae) were collected during the post-flood survey (Fig. 6a). Copepods were more abundant at more isolated sites. Other crustaceans and mosquito larvae were found only at “Isolated” and “No flow” sites. The model comparison showed that flow on 15 May (peak flow) best explained zooplankton density, and flow cessation on 23 May best explained zooplankton diversity (Table 1).

A total of 3789 individual benthic macroinvertebrates belonging to 37 families (32 aquatic insect families and 5 others) were counted (Fig. 6b). Chironomidae were the most common. The number of families was highest at "Flowing" sites, and 15 families were found only at “Flowing” sites. The model comparison showed that flow on 15 May (peak flow) best explained the density of benthic macroinvertebrates, and flow on 11 June (low flow, time at sampling) best explained their diversity (Table 1).

A total of 559 individual fish belonging to nine species were found during the post-flood survey (Fig. 4). *Salvelinus leucomaenis* (Salmonidae) occurred at the highest density, 50.2% of all captured individuals, followed by stone loach (*Noemacheilus barbatulus*), Asiatic brook lamprey (*Lethenteron reissneri*), and Masu salmon (*Oncorhynchus masou*). Fish density was negatively associated with habitat area, possibly owing to higher competition (Nakano, 1995) or lower capturing efficiency in large habitats. Importantly, the model comparison showed that flow on 15 May (peak flow) best explained both fish density and diversity (Table 1).

Only two species of amphibians, *Rana pirica* and *Hynobius retardatus*, were observed during the present study. The model comparison showed that the presence of amphibian eggs was best explain by flow cessation on 23 May (and secondarily by flow on 28 May) (Table 1); thus, the timing of flow cessation determined whether eggs of these amphibian species were present.

When all of the biological data, including those for the four faunal groups, were considered altogether, the NMDS biplot showed clear differences in the biota along the gradient of connectivity to the main stream (Fig. 7a; Fig. S2), and the PERMANOVA results also showed significant variation of the biota in relation to the connectivity gradient (Table S2). The SIMPER results showed different contributions of the four faunal groups to the variation of the biota along the connectivity gradient (Fig. 7b; Table S3): The contribution of plankton to the separation of Isolated and No flow sites from other sites was high, whereas the contribution of amphibians to the separation of Early, Middle, and Late sites was high. Benthic macroinvertebrates contributed greatly to the separation of Flowing sites from other sites, whereas fish contributed equally to the variations among the sites except at the Flowing sites.

4 DISCUSSION

Environmental shifts occurred asynchronously among the waterbodies of the floodplain, and the hydrological dynamics of each waterbody influenced the local community composition. The flood-recession survey showed that the four aquatic faunal groups (plankton, benthos, fish, and amphibians) responded dynamically but differently to the hydrological changes over the flood recession period. The post-flood survey showed that the distribution patterns of the four faunal groups differed according to the hydrological dynamics over the flood period, as was predicted from the different biological responses of each faunal group to the hydrological conditions. Our results indicate that the distinct responses of each biological group to conditions during the spring flood were responsible for their respective post-flood distribution patterns in the waterbodies. Our overall results support our hypothesis that the spatial asynchrony in channel isolation from the main stream during flood recession results in diverse aquatic communities on the floodplain, and that the different responses of the various faunal groups to the hydrological dynamics drives that diversity.

The temporal dynamics of nutrient concentrations and phyto- and zooplankton over the flood recession period showed that plankton bloomed in isolated waterbodies never flushed by flowing floodwaters, and that the nutrients became depleted in such isolated waterbodies over time. The lower nutrient concentrations (NO_3^- and SRP) in waterbodies with high densities of phyto- and zooplankton indicate that plankton density was limited by factors other than nutrient availability, and that in isolated waterbodies nutrients were depleted by plankton (Van Den Brink et al., 1992). Plankton communities are known to be vulnerable to flow (Chaparro et al., 2018; Van den Brink et al., 1994); thus, in many of the waterbodies, phyto- and zooplankton were likely flushed by the floodwaters. However, the emergence of plankton in waterbodies that had been flushed indicates that some plankton somehow remained in these waterbodies during the flood period (Frisch, 2002) or that they colonized them after the flood (Jenkins & Boulton, 2003). Although in each waterbody the plankton density started to increase once the flow stopped, and it is possible that later in the low-flow season (i.e., after the study period) their density would become higher (Baranyi et al., 2002; Grosholz & Gallo, 2006; Schagerl et al., 2009), their recovery was not fast enough to compensate for the impacts of the flow at flood peak by the time of sampling.

In contrast to plankton, fish were more abundant and diverse in waterbodies that were flushed by the peak flow. The spatial match between the stable carbon isotope ratios of fish fry and benthos, together with the similarity of the fish species composition at each site between the flood-recession and post-flood surveys, indicates that the residency of fish fry in each palaeo-side channel was high. Salmonids spawn in habitats with gravel and pebble substrates (Montgomery et al., 1999), which are common in the main stream and side channels of the studied system. Furthermore, most of the fish in the floodplain waterbodies (palaeo-side channels) were juveniles; adults were found only in the main stream. Fitzgerald et al. (2021) estimated that the dominant species in the studied system, *Oncorhynchus masou* and *Salvelinus leucomaenis*, hatch primarily in February and March. Therefore, it is assumed that salmonid fry that hatched in extant side channels or the main stream of the river moved to the palaeo-side channels during the flood to continue their development as described by Rosenfeld et al., (2008), whereas those hatched in extant side channels during the summer low-flow period remained there during their development. Floodplain waterbodies are important nurseries for many fishes in the river (Jeffres, Opperman & Moyle, 2008; Bellmore et al., 2013), and they out-migrate from side channels to the river and sometimes to downstream lakes as they grow (Tamate & Maekawa, 2004; Kanno et al., 2020). Although fish diversity was lower in waterbodies with lower connectivity, we observed some fish species in those waterbodies that were not found in the more connected waterbodies. Species that occurred in isolated waterbodies included Cyprinidae and Cobitidae, which are known to tolerate anoxic conditions (Fagernes et al., 2017). The spatial variation in hydrological dynamics over flood recession period thus contributed to the diversity of fish fauna on the floodplain.

Interestingly, the presence of amphibians was determined by the timing of flow cessation in each waterbody. Both amphibian species reproduced in the floodplain waterbodies soon after the flood peak, and their eggs hatched and larvae developed in the waterbodies during the low-flow period, a common pattern in amphibians (Griffiths, 1997; Tockner et al., 2006; Holgerson et al., 2019). Our post-flood survey showed that amphibian eggs were laid and larvae were observed in waterbodies where the flow had stopped in the early flood recession period, before their reproductive season. Waterbodies on the floodplain provide important habitats for amphibian larvae, yet use of this temporary habitat exposes them to various risks, including desiccation (Gervasi & Foufopoulos, 2008) and being flushed by flow (Indermaur et al., 2010). Therefore, the timing of environmental shifts such as flood recession may be particularly important for amphibians, which use the floodplain waterbodies only seasonally.

Finally, benthos distributions were greatly influenced by the occurrence of flow at the time of sampling. We observed diverse aquatic insect taxa, including Ephemeroptera, Plecoptera, and Trichoptera, in flowing waterbodies; most of these taxa require flowing water for respiration (Merrit, Cummins & Berg, 2008), and they were not found in more isolated floodplain waterbodies. In contrast, Chironomidae dominated most of the floodplain waterbodies in this study. Relatively low Chironomidae density in isolated waterbodies, which were not flushed by flow at peak flood, in contrast to other floodplain waterbodies may be explained by the extremely anoxic conditions of benthic habitats in those waterbodies. The low δ^{13}C (–40‰) of benthos in isolated waterbodies indicates that benthic conditions were so anoxic that methane-derived carbon was consumed by the benthos (Kohzu et al., 2004). In this study, we sorted benthos at the family level, but species level identification could have shown spatial variation of Chironomidae according to the hydrological dynamics over flood.

Overall, the observed unique responses of the four faunal groups to the hydrological dynamics over the snowmelt flood recession period well explained the spatial distributions of the four faunal groups on a floodplain. This indicates spatial asynchrony in channel isolation from the main stream during flood recession and responses of the four biological groups led their distinct distributions on a floodplain. We however acknowledge the difficulties in clearly teasing out the effect of spatial variation in hydrological dynamics over the flood recession period we focused in this study from the effect of spatial variations in local environmental conditions (such as dissolved oxygen, pH, and substrate type). Future experimental studies would be required to clearly distinguish among these factors. Furthermore, the four faunal groups that are individually presented in this study interact with each other through food webs. Diverse aquatic communities on the floodplain observed in this study indicate that food web structures are also variable. Further studies of community structures and species interactions in relation to hydrological dynamics would provide insights into the dynamic meta-community (Leibold et al., 2004) and meta-ecosystem structures (Gounand et al., 2018) on a floodplain.

Our results supported the findings of previous studies that showed the link of hydrological connectivity to the river and the floodplain aquatic communities (Tockner et al., 2000; Amoros & Bornette, 2002). Moreover, the results of our studies during the flood period showed how hydrological dynamics during the flood shaped the distribution of each faunal group: plankton and fishes were primarily influenced by whether the waterbody was flushed by peak flow, whereas amphibians were influenced by the timing of flow cessation and continuing flow during low-flow periods was important for benthos. Advanced technology for surveying the environment on broad spatial and temporal scales is now readily available, including time-lapse photography (Parajka et al., 2012), drones (Woodget et al., 2017), and remote sensing (Arnesen et al., 2013). By using these techniques to monitor the hydrological dynamics on floodplains over the flood period, together with our mechanistic understanding of the biological responses to hydrological dynamics, it should be possible to predict the spatial distribution of aquatic communities on floodplains.

Spatially variable hydrological dynamics and the biological responses on the floodplain were supported by a combination of the natural geomorphic complexity of the floodplain and the natural seasonal dynamics of river discharge over the snowmelt recession period. This study showed that three components of the seasonal river flow dynamics played particularly important roles in supporting diverse aquatic communities: the peak flood stage, flow at low stage, and the timing of flow recession. The magnitude and timing of the snowmelt flood shows substantial year-to-year variations (Yarnell et al., 2010). Long-term monitoring of the floodplain biota may reveal interannual habitat shifts of the aquatic community on a floodplain caused by variation of the hydrological dynamics of the snowmelt recession. Factors such as climate change and regulation by dam construction can also change the seasonal dynamics of river discharge (Poff & Schmidt, 2016; Yarnell et al., 2010). The results of this study highlight the importance of the natural hydrological dynamics of snowmelt recession on floodplain communities.

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Conflicts of Interest Statement

The authors declare no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Legends

Table 1: Model selection to reveal the threshold of connectivity to the river that influences the density and diversity of each faunal group. Bold numbers indicate the lowest AIC of each row.

Figure 1: Locations of the flood-recession and post-flood survey sites with different connectivity to the main stream of the Butokamabetsu River, Hokkaido, Japan. Spatial sampling was conducted at 26 palaeo- or extant side channels of the Butokamabetsu River (coloured circles) distributed along a 10 km segment of the river and divided into five blocks. The flood-recession survey was conducted at four focal sites (sites A–D; bold circles).

Figure 2. Seasonal hydrological changes of the Butokamabetsu River. (a) Total discharge of the Butokamabetsu River from 1 April to 1 July 2019. (b) Examples of spatial changes in hydrological connectivity and flow of various palaeo- and extant side channels during the spring snowmelt and flood recession. (c) The six categories of hydrological connectivity used in this research. Sampling sites were assigned to a hydrological connectivity category based on repeated observations of hydrological connectivity and flow at each site. (d) Changes in flow speed at the four focal sites where the flood-recession survey was conducted.

Figure 3: Spatial variation (left column; post-flood survey) and temporal variation (right column; flood-recession survey) of water chemistry and plankton density. In the graphs in the left column, each symbol (or bar for Zooplankton) shows the average value of multiple sites

with the same connectivity index, and the error bars show ± 1 standard error among the sites. The right panels show the temporal variation of the data at the four focal sites and one main stream site measured during the flood-recession survey.

Figure 4: Fish species composition at the focal sites during (22 May) and after (12 June) the spring snowmelt flood. Each colour represents a different species, as indicated in the legend. For salmonids, young of the year individuals (YOY) were counted separately, and their densities are indicated hatching.

Figure 5: Stable carbon isotope ratios of benthos and fish at the focal sites and the mainstream site. Each data point shows the average $\delta^{13}C$ of benthos (*x*-axis) and $\delta^{13}C$ of fish (*y*-axis) at one site. The error bars indicate ± 1 standard error of individual variations within each site. The dashed line shows the fitted regression line along the connectivity gradient.

Figure 6: Spatial variation of density and diversity of the four faunal groups in the post-flood sampling. Each bar indicates the average density of each faunal group at multiple sites with the same connectivity to the river. Circles indicate the average taxa richness of each faunal group at multiple sites with the same connectivity. The error bars indicate ± 1 standard error among sites. Black inverted triangles indicate primary and secondary (ΔAIC < 4) thresholds of faunal density, and white inverted triangles indicate the thresholds of faunal diversity based on the model selection results shown in Table 1.

Figure 7: (a) Nonmetric multidimensional scaling (NMDS) ordination of the whole aquatic biota (including the four faunal group) at each of the 26 sites sampled during the post-flood survey. Sites are coloured according to their connectivity to the river. Each polygon represents a convex hull created by connecting the outermost site scores for each of the six connectivity levels. Data for the four faunal groups were combined after standardization. (b) Results of similarity percentage analysis (SIMPER). Vertical axis shows the total contribution of each faunal group to the variation in the aquatic biota between connectivity thresholds.

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Faunal group	Factor	Unit	15 May River connection (AIC)	15 May Flow (AIC)	23 May Flow (AIC)	28 May Flow (AIC)	11 June Flow (AIC)	Best fit model	Estimate	SE	t-value	p-value	Note
Zooplankton	Density	ind L^{-1}	257.6	**251.9**	256.3	258.4	258.5	15 May Flow	-40.1	13.4	-3	<0.01	
	Diversity	# of families	95.6	81	**75.6**	89.4	91.9	23 May Flow	-1.8	0.29	-6.1	<0.001	
Benthos	Density	ind m^{-2}	385.6	**384.9**	389	389	389	15 May Flow	550.7	225.6	2.4	<0.05	
	Diversity	# of families	141.5	136.5	140.1	140	**124.8**	11 June Flow	7.24	1.37	5.29	<0.001	
Fish	Density	ind m^{-2}	35.3	**31.7**	34.1	35.7	37.9	15 May Flow	0.32	0.11	2.9	<0.01	*
	Diversity	# of species	112.4	**109.7**	116.1	117.1	116.6	15 May Flow	1.9	0.57	3.31	<0.01	
Amphibian	Presence rate		84.1	79.5	**69.8**	71.5	79.6	23 May Flow	-1.24	0.25	-5	<0.001	
	Diversity	# of species	84.1	79.5	**69.8**	71.5	79.6	23 May Flow	-1.24	0.25	-5	<0.001	

* significant effect of sampling area: Estimate=-0.00093, SE=0.00042, t-value=-2.2, p-value<0.05

Table1

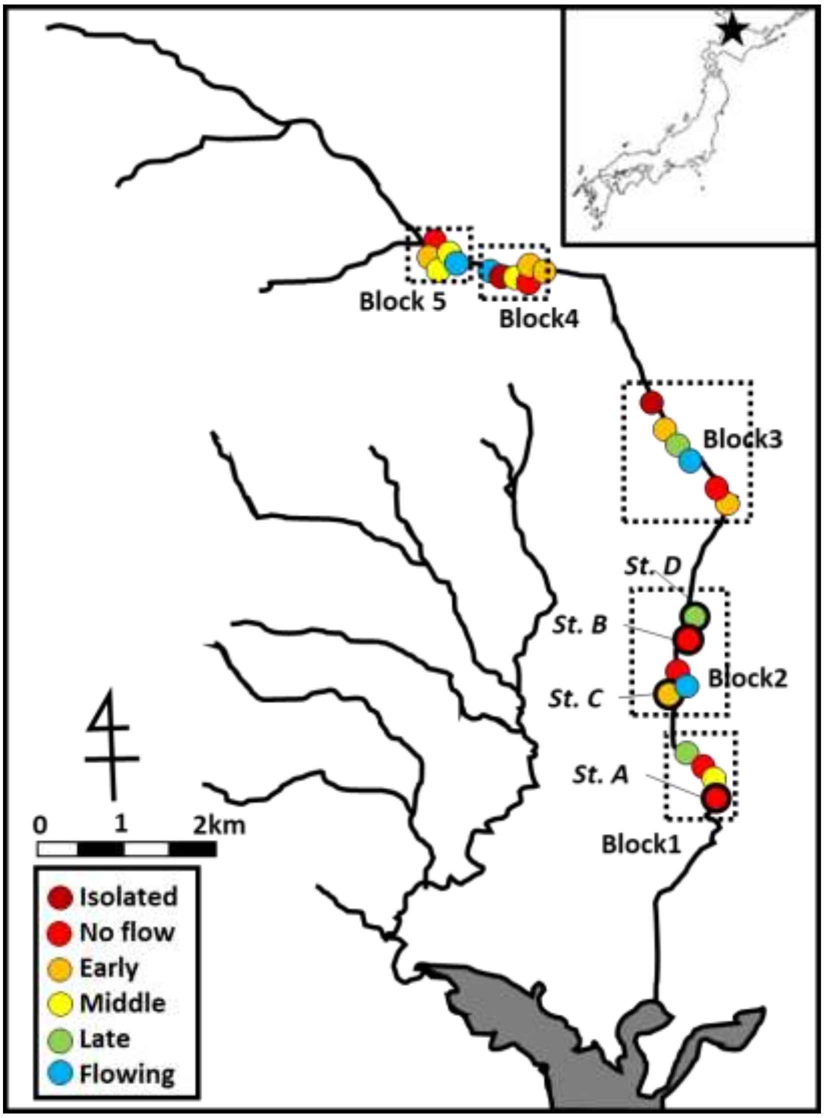
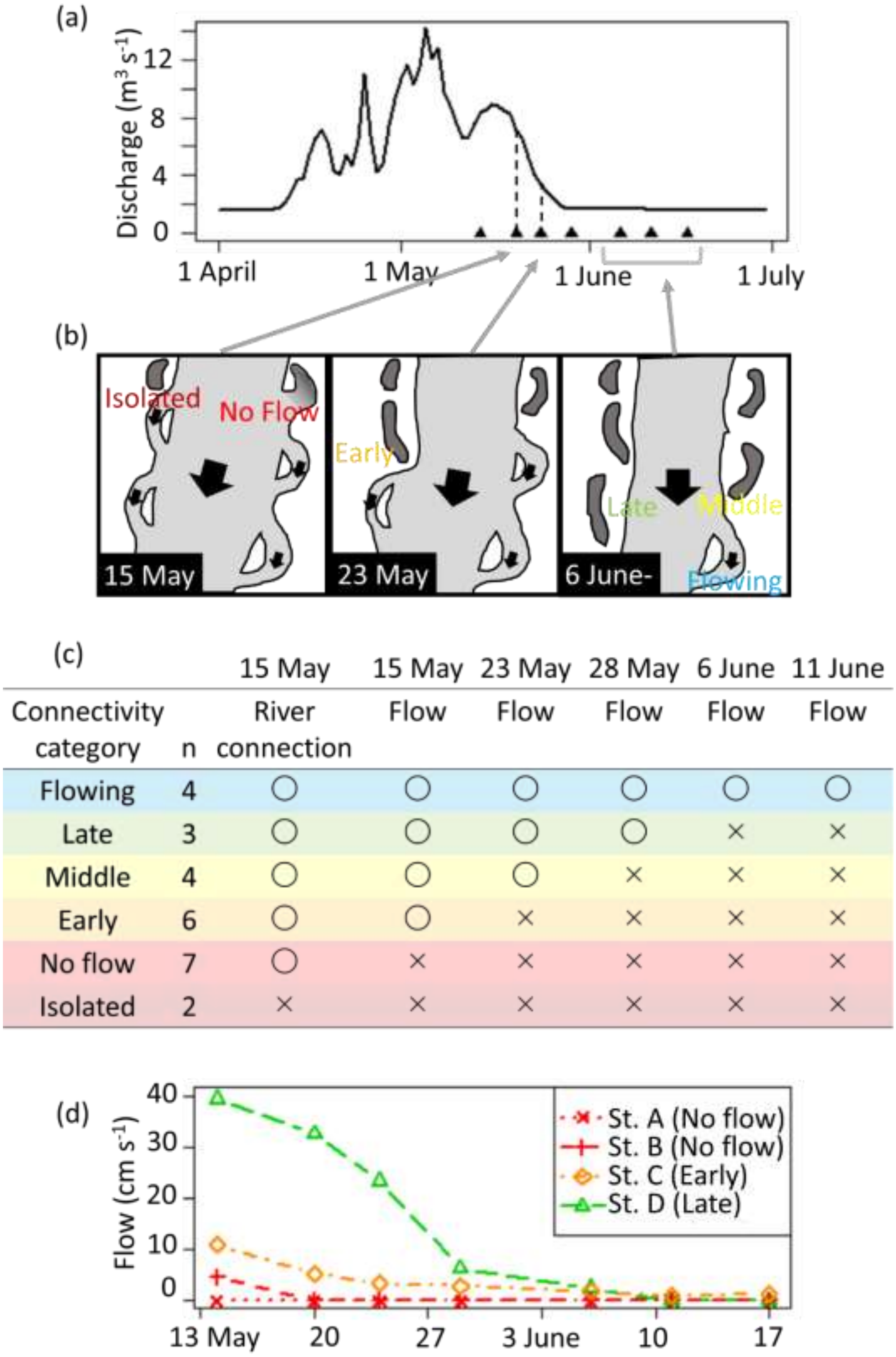

Block 5
Block4
Block3
St. D
St. B
Block2
St. C
St. A
Block1
0
1
2km
Isolated
No flow
Early
Middle
Late
Flowing

Figure1



Connectivity category	n	15 May River connection	15 May Flow	23 May Flow	28 May Flow	6 June Flow	11 June Flow
Flowing	4	○	○	○	○	○	○
Late	3	○	○	○	○	×	×
Middle	4	○	○	○	×	×	×
Early	6	○	○	×	×	×	×
No flow	7	○	×	×	×	×	×
Isolated	2	×	×	×	×	×	×

Figure 2

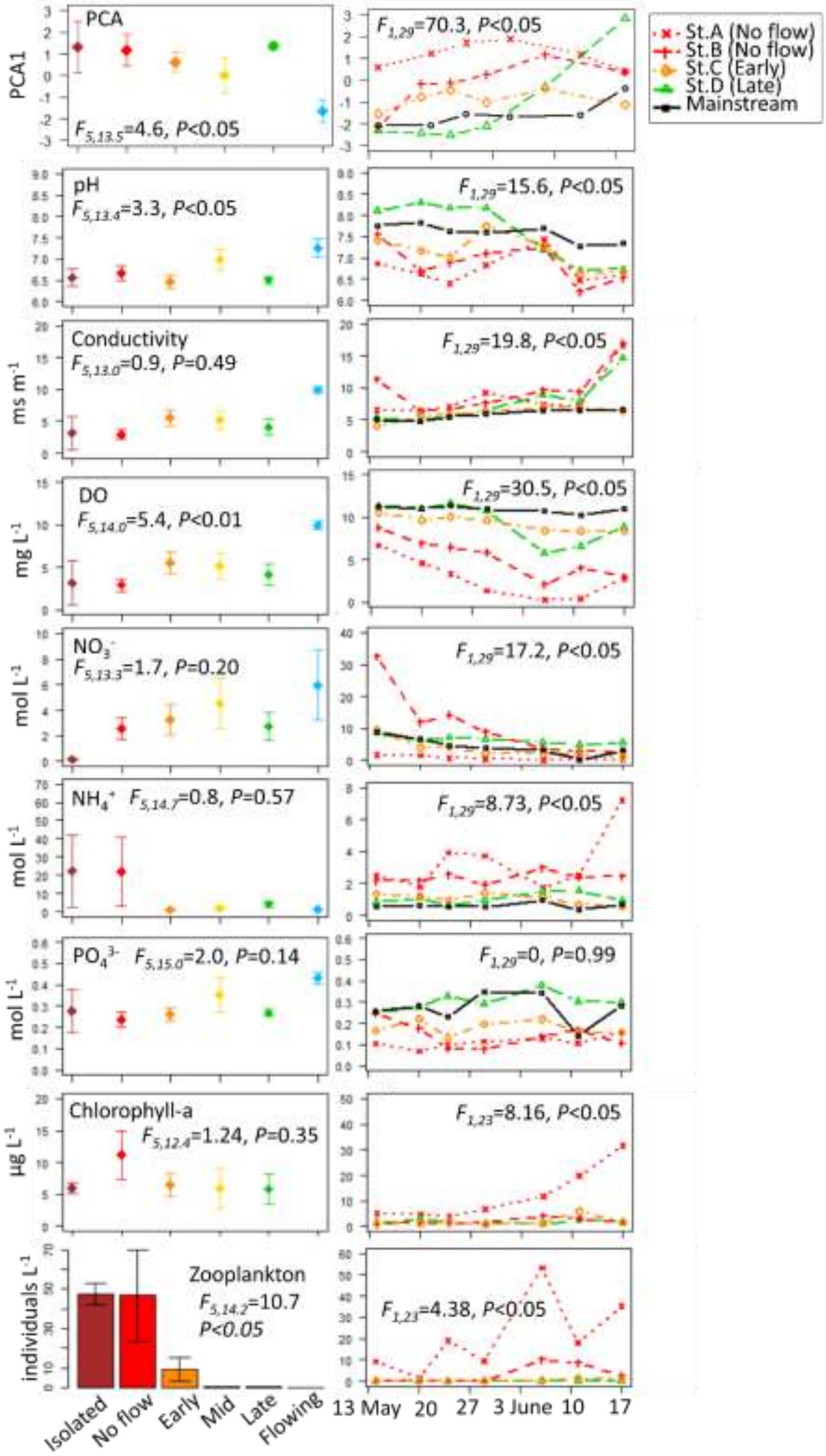
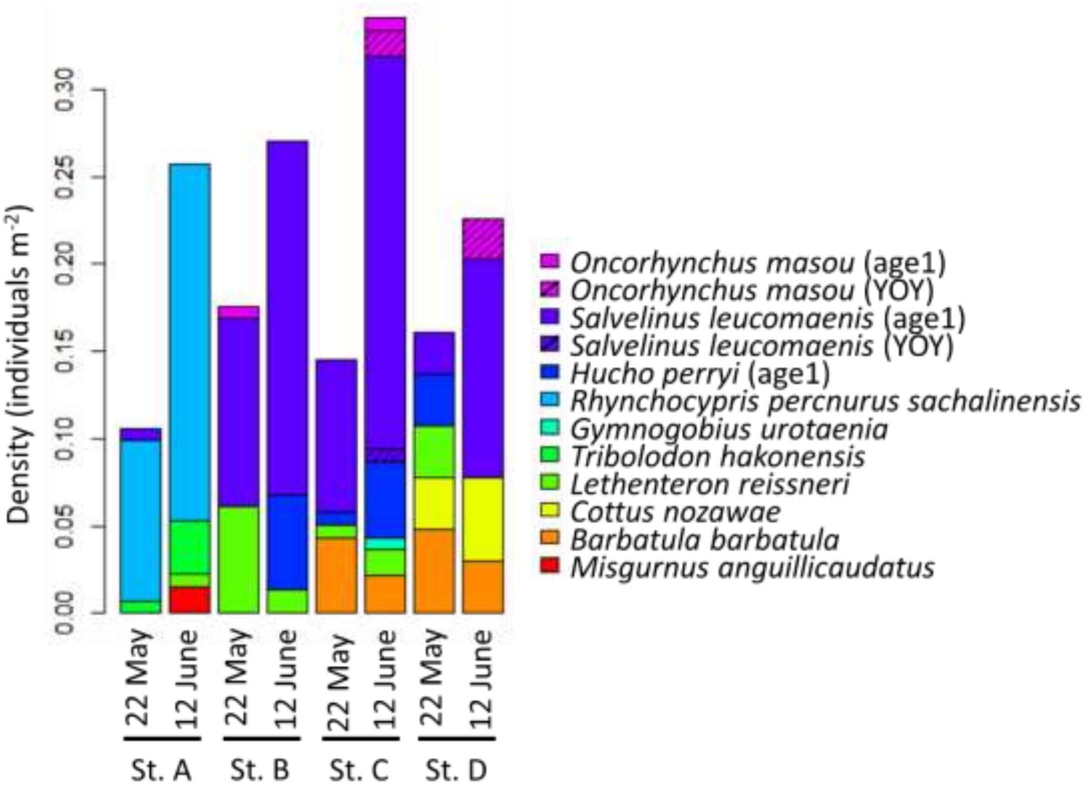

PCA
PCA1
$F_{5,13.5}$=4.6, P<0.05
$F_{1,29}$=70.3, P<0.05
St.A (No flow)
St.B (No flow)
St.C (Early)
St.D (Late)
Mainstream
pH
$F_{5,13.4}$=3.3, P<0.05
$F_{1,29}$=15.6, P<0.05
Conductivity
ms m^{-1}
$F_{5,13.0}$=0.9, P=0.49
$F_{1,29}$=19.8, P<0.05
DO
mg L^{-1}
$F_{5,14.0}$=5.4, P<0.01
$F_{1,29}$=30.5, P<0.05
NO_3^-
mol L^{-1}
$F_{5,13.3}$=1.7, P=0.20
$F_{1,29}$=17.2, P<0.05
NH_4^+
mol L^{-1}
$F_{5,14.7}$=0.8, P=0.57
$F_{1,29}$=8.73, P<0.05
PO_4^{3-}
mol L^{-1}
$F_{5,15.0}$=2.0, P=0.14
$F_{1,29}$=0, P=0.99
Chlorophyll-a
µg L^{-1}
$F_{5,12.4}$=1.24, P=0.35
$F_{1,23}$=8.16, P<0.05
Zooplankton
individuals L^{-1}
$F_{5,14.2}$=10.7
P<0.05
$F_{1,23}$=4.38, P<0.05
Isolated
No flow
Early
Mid
Late
Flowing
13 May
20
27
3 June
10
17

Figure 3

821



822
823
824 Figure 4
825

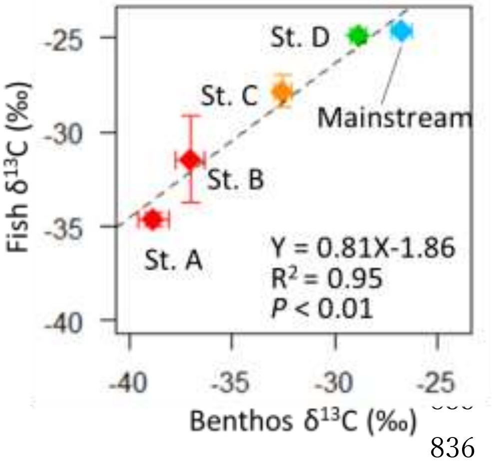

St. D
St. C
Mainstream
St. B
St. A
Y = 0.81X-1.86
R2 = 0.95
P < 0.01
-25
-30
-35
-40
Fish δ13C (‰)
-40
-35
-30
-25
Benthos δ13C (‰)

Figure 5

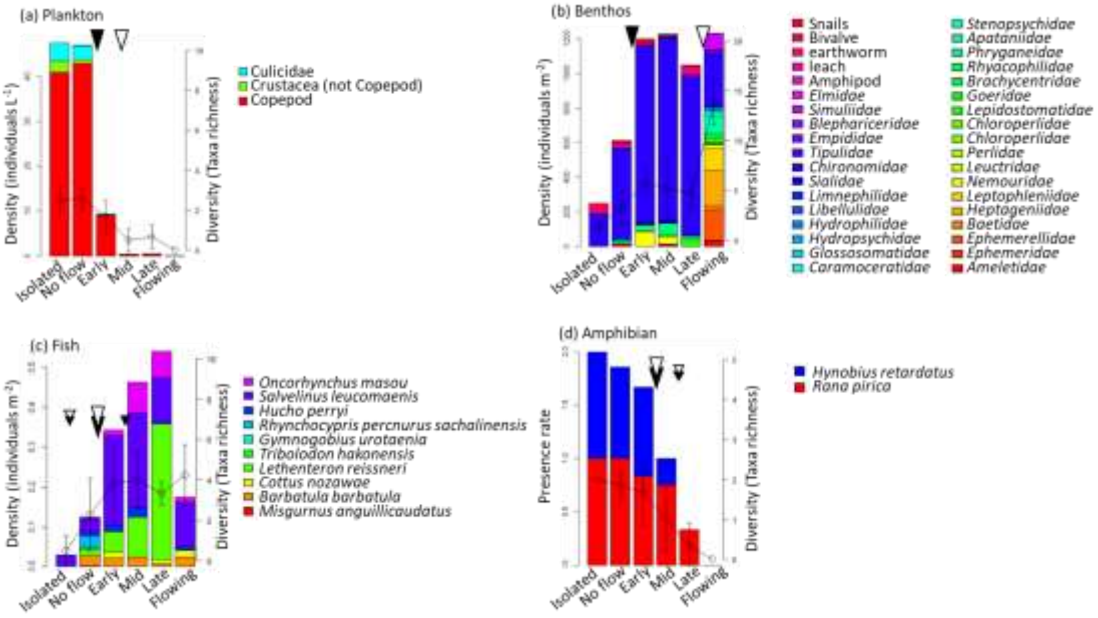

(a) Plankton
Density (individuals L^{-1})
Diversity (Taxa richness)
Isolated
No flow
Early
Mid
Late
Flowing
Culicidae
Crustacea (not Copepod)
Copepod
(b) Benthos
Density (individuals m^{-2})
Diversity (Taxa richness)
Isolated
No flow
Early
Mid
Late
Flowing
Snails
Bivalve
earthworm
leach
Amphipod
Elmidae
Simuliidae
Blephariceridae
Empididae
Tipulidae
Chironomidae
Sialidae
Limnephilidae
Libellulidae
Hydrophilidae
Hydropsychidae
Glossasomatidae
Caramoceratidae
Stenopsychidae
Apataniidae
Phryganeidae
Rhyacophilidae
Brachycentridae
Goeridae
Lepidostomatidae
Chloroperlidae
Chloroperlidae
Perlidae
Leuctridae
Nemouridae
Leptophleniidae
Heptageniidae
Baetidae
Ephemerellidae
Ephemeridae
Ameletidae
(c) Fish
Density (individuals m^{-2})
Diversity (Taxa richness)
Isolated
No flow
Early
Mid
Late
Flowing
Oncorhynchus masou
Salvelinus leucomaenis
Hucho perryi
Rhynchocypris percnurus sachalinensis
Gymnogobius urotaenia
Tribolodon hakonensis
Lethenteron reissneri
Cottus nozawae
Barbatula barbatula
Misgurnus anguillicaudatus
(d) Amphibian
Presence rate
Diversity (Taxa richness)
Isolated
No flow
Early
Mid
Late
Flowing
Hynobius retardatus
Rana pirica

Figure 6

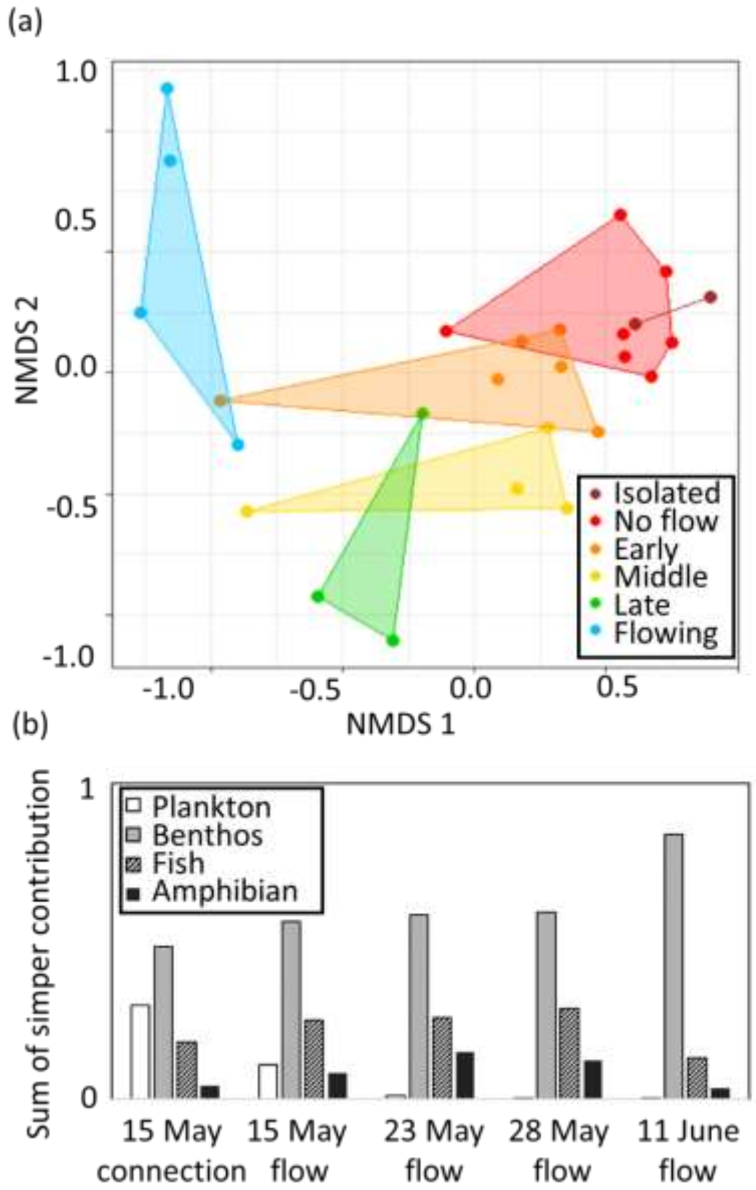

(a)
1.0
0.5
0.0
-0.5
-1.0
NMDS 2
-1.0
-0.5
0.0
0.5
NMDS 1
● Isolated
● No flow
● Early
● Middle
● Late
● Flowing
(b)
Sum of simper contribution
1
0
□ Plankton
▨ Benthos
▨ Fish
■ Amphibian
15 May connection
15 May flow
23 May flow
28 May flow
11 June flow

Figure 7