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1 ***Freshwater Biology***

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

4  
5 **Running head: Flood shape diverse aquatic communities**

6  
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27  
28 **Keywords**

29 floodplain; snowmelt recession; spatial heterogeneity; hydrological dynamics; biodiversity

30  
31  
32 **Abstract**

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

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

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

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

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

68

## 69 **1 INTRODUCTION**

70 Floodplains are one of the most dynamic landscape ecosystems. Many waterbodies on  
71 floodplains are formed by fluvial processes such as channel migration and abandonment. Extant  
72 and palaeo-side-channels, a representative waterbody type on floodplains, have diverse degrees

73 of hydrological connectivity to a river's main stream: some are permanently connected to the  
74 river, some are connected to the river only at times of high flow, and others are never connected  
75 to the river (Amoros & Roux, 1988). In many temperate floodplains, spring snowmelt causes  
76 long-lasting floods that seasonally expand and gradually contract river channels, thus supporting  
77 spatially and temporally dynamic aquatic habitats for various faunal groups, including plankton,  
78 benthos, nekton (fish), and amphibians (Tockner, Malard & Ward, 2000).

79

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

101

102 Different responses of different faunal groups to the hydrological dynamics over flood periods  
103 may drive the diversity of aquatic communities in floodplain waterbodies. In floodplain  
104 waterbodies, we observe at least four biological groups, namely, plankton, benthos, nekton  
105 (fish), and amphibians, whose responses to the hydrological dynamics should differ according to  
106 their ecological characteristics. For example, limitations to dispersal and migration may be  
107 critical for mobile organisms such as fish (Bolland et al., 2012; Crook et al., 2020). Flow pulses  
108 during flood periods may have a large influence on plankton, which might be flushed

109 downstream by floodwaters (Van den Brink, Van Katwijk & Van der Velde, 1994), and on  
110 benthos, through mobilization of substrate materials (Arscott, Tockner & Ward, 2005). A  
111 growing number of studies have addressed the use of floodplain habitats by different taxonomic  
112 or faunal groups (Van den Brink et al., 1994; Morand & Joly, 1995; Bolland et al., 2012;  
113 Gallardo et al., 2014), but only a few studies have simultaneously examined the distributions of  
114 the distinct faunal groups that inhabit a river-floodplain system (Tockner, Schiemer & Ward,  
115 1998). However, given that hydrological dynamics influences each faunal group differently, by  
116 focusing on a single faunal group, the critical environmental gradient that is required to support  
117 diverse aquatic communities may be underestimated. Variation in responses to hydrological  
118 dynamics among faunal groups is one factor that supports diverse aquatic communities on a  
119 floodplain, and gradients that include a wider range of hydrological environments may support  
120 more diverse aquatic communities.

121

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

139

## 140 **2 METHODS**

### 141 **2.1 Study system**

142 The study was conducted on the Butokamabetsu River floodplain, located in the Hokkaido  
143 University Uryu Experimental Forest, northern Japan (44°24'N, 142°07'E) (Fig. 1). The  
144 floodplain is covered predominantly by 1–2 m high broad-leaf bamboo (*Sasa senanensis*) and a

145 sporadic mix of deciduous trees such as alder (*Alnus japonica*) and Japanese white birch (*Betula*  
146 *platyphylla*). Some wetlands and some areas of humic soils are distributed on the floodplain  
147 (Shibata et al., 2004; Ogawa et al., 2006). The main stream of the Butokamabetsu River, which  
148 is about 10 m wide under summertime low-flow conditions, has many extant and palaeo-side  
149 channels. Extant side channels remain connected to the main stream even during periods of low  
150 flow and the water remains flowing all year around. Palaeo-side channels are old side channels  
151 that have become isolated from the main stream through the loss of their upstream connection  
152 with the river as a result of fluvial sediment and debris accumulation and flood dynamics. Many  
153 palaeo-side channels, including our study sites, harbour stagnant water during low flow (also  
154 called oxbow lakes). Floodwater flows into some of the palaeo-side channels at high flow, and  
155 the water keeps flowing through palaeo-side channels until the river water level drops to certain  
156 levels for respective paleo-side channel depending on their geomorphology. Therefore, a  
157 gradient of hydrological connectivity to the river exists among waterbodies on the floodplain:  
158 extant side channels, seasonally connected palaeo-side channels, and permanently isolated  
159 palaeo-side channels.

160

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

169

## 170 **2.2 Flood-recession survey**

171 We conducted a flood-recession survey to characterize the temporal dynamics of hydrology and  
172 water chemistry, as well as the biological responses of the four faunal groups to the  
173 environmental changes as floodwater receded. As focal study sites for the flood-recession  
174 survey, we selected four representative waterbodies with different degrees of connectivity to the  
175 mainstream river (Fig. 2): “No flow” sites A and B, a “Early” site C, and a “Late” site D, as  
176 determined during the post-flood survey (see section 2.4). At these four focal sites and at one  
177 mainstream site (site E), we recorded environmental data approximately every five days from 14  
178 May through 17 June 2019. At each site, we measured pH and conductivity with a portable  
179 pH/COND meter (D-74, HORIBA, Kyoto, Japan) and dissolved oxygen and water temperature  
180 with a portable multimeter (HQ-30d, HACH, Loveland, Colorado, USA). We collected a 200-ml

181 water sample in prewashed polyethylene bottles for nutrient analysis. Water samples were  
182 filtered through a GF/F filter within 24 h, and both the GF/F filter and the filtered water were  
183 frozen for later chlorophyll-*a* analysis (as an indicator of phytoplankton density) and nutrient  
184 analysis in the laboratory. Furthermore, 20 L of water was filtered through a 70- $\mu$ m-mesh  
185 plankton net and preserved in Lugol solution for zooplankton analysis.

186

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

197

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

201

### 202 **2.3 Isoscape analysis of the stable carbon isotope ratio**

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

216 than those of their prey items. Further, if only some fish have moved between waterbodies, then  
217 stable carbon isotope ratios should exhibit large variation among individuals.

218

219 We collected fish and their potential prey items at the four focal sites at the end of the recession  
220 period. We collected representative benthic invertebrates with dip nets on 17 June 2019. At each  
221 site, we collected 7 to 13 individuals belonging to 12 taxa. We collected most fish samples  
222 during the second fish survey on 12 June 2019 (see section 2.2). We collected two  
223 supplementary fish samples from site B on 19 June 2020, together with benthic  
224 macroinvertebrate specimens. We confirmed that the stable carbon and nitrogen isotope ratios  
225 did not differ significantly between sampling years; thus, we pooled the data from 2019 and  
226 2020 for the isoscape analysis. We collected 2 to 10 individuals of the dominant fish species at  
227 each site for stable isotope analysis. All fish and benthic invertebrate samples were immediately  
228 frozen and transported to Kyoto University for later analysis.

229

#### 230 **2.4 Post-flood Survey**

231 To examine how the biological responses during the flood, observed in the flood-recession  
232 survey, shaped the spatial distribution of the aquatic biota at low flow (post-flood), we  
233 conducted a post-flood survey of waterbodies on 12–13 June 2019, after snowmelt had ceased.  
234 A total of 26 waterbodies (including both palaeo- and extant side channels) with different  
235 degrees of connectivity to the main stream in five spatial blocks along a 10-km segment of the  
236 Butokamabetsu River were selected (Fig. 1). We confirmed that there was no significant bias in  
237 the distribution of connectivity among the blocks (one-way analysis of variance [ANOVA];  $P =$   
238 0.95). Before the post-flood survey, during and after the flood recession from early May to mid-  
239 June, we visited each site every five days to record its connectivity to the river's main stream.  
240 During these visits, we visually examined the surface water connection to the main stream at  
241 both the upstream and downstream ends of each waterbody. When there were surface water  
242 connection upstream, mainstream river water flew-in from the upstream end, flew through the  
243 waterbodies, and flew-out from the downstream end. Therefore, in all cases when we observed  
244 upstream connection in this study, we also observed downstream connection, and the  
245 waterbodies were flushed by flow. In contrast, downstream connection did not make as much  
246 influence on the physical environment of the entire waterbodies as the upstream connection.  
247 Yet, we assumed the downstream connection could enable the immigration and emigration of  
248 fishes. Based on these observations, we categorized the study sites into six connectivity  
249 categories (Figs. 1, 2). "Isolated" sites were never connected to the river, even at peak discharge.  
250 "No flow" sites were never flushed by floodwaters, because the upstream end of the palaeo-side  
251 channel was always closed, but at flood peak they were hydrologically connected to the main



252 stream at their downstream end. At the "Early", "Middle", and "Late" sites, each waterbody was  
253 flushed by flow at peak discharge and isolated from the main stream at low flow, but differed by  
254 the timing of flow cessation. At "Early", "Middle", and "Late" sites, flow cessation occurred on  
255 23 May, 28 May, and 6 June 2019, respectively. At "Flowing" sites, flow was continuous  
256 throughout the study period. Among the 26 sites, 2 were categorized as "Isolated", 7 as "No  
257 flow", 6 as "Early", 4 as "Middle", 3 as "Late", and 4 as "Flowing" sites.

258

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

269

## 270 **2.5 Laboratory analysis**

271 All analyses were conducted at the Center for Ecological Research, Kyoto University, Otsu,  
272 Japan. Nitrate ( $\text{NO}_3^-$ ) nitrogen was quantified by first reducing nitrate to nitrite using a cadmium  
273 coil followed by diazotization with sulfanilamide and coupling with *N*-(1-naphthyl)  
274 ethylenediamine dihydrochloride. Ammonium ( $\text{NH}_4^+$ ) nitrogen was quantified by the  
275 indophenol blue method. Soluble reactive phosphorous (SRP) was quantified by the  
276 molybdenum blue method. A continuous flow auto-analyser (QuAatro 2-HR, BLTEC, Osaka,  
277 Japan) was used for these analyses.

278

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

284

285 Stable carbon and nitrogen isotope analyses were also conducted at the Center for Ecological  
286 Research, Kyoto University. Benthic insect samples were freeze-dried, and their whole bodies  
287 were individually ground prior to the analysis. For fish samples, a sample of muscle tissue was

288 dissected out, then freeze-dried and ground for the analysis. A subsample of fish muscle tissues  
289 was immersed in chloroform/methanol (2:1) solution for 24 h and then rinsed with methanol to  
290 remove lipids. Stable nitrogen isotope ratios of samples without lipid removal and stable carbon  
291 isotope ratios of samples after lipid removal were used as the representative values of fish  
292 muscle, as described by Sotiropoulos, Tonn & Wassenaar (2004). Stable carbon and nitrogen  
293 isotopes were measured with an elemental analyzer/isotope ratio mass spectrometer (EA/IRMS;  
294 DELTA-V plus, Thermo Fisher Scientific, United States).. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ )  
295 isotope ratios are expressed as the per mil (‰).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of standard samples and the  
296 analytical methods described above were referenced from Tayasu et al. (2011).

297

## 298 **2.6 Data analysis**

299 To examine spatial and temporal variations in water chemistry, we conducted a principal  
300 component analysis (PCA) of pH, conductivity, DO,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$  and SRP data collected at all  
301 sites in all seasons. To examine the spatial variation in water chemistry during the post-flood  
302 survey, scores on the first PCA axis (PCA1) were compared with the connectivity of each site,  
303 where spatial block was included as a random factor in a linear mixed model, by using the lmer  
304 function in the lme4 package (Bates et al., 2021) and the anova function in the lmerTest package  
305 (Kuznetsova et al. 2020) in the R software environment (R Core Team, 2018). To examine  
306 differences in the temporal variation in water chemistry at among the four focal sites with  
307 different degrees of connectivity to the main stream, we compared the PCA1 score of the focal  
308 sites with the Julian date by one-way ANOVA, including sampling site as a random factor.  
309 Additionally, the same analyses were conducted for pH, conductivity, DO,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and  
310 SRP, as well as chlorophyll *a* and zooplankton density. To compare the temporal shift in fish  
311 species composition from the peak flood to the end of the flood season and the spatial variation  
312 of fish species composition across waterbodies, we performed permutational multivariate  
313 analysis of variance (PERMANOVA) using the adonis function in the vegan package (Oksanen  
314 et al., 2020). Plankton and fish density data were log-transformed prior to all analysis.

315

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

320

321 Using the post-flood survey data, we examined how the temporal hydrological dynamics  
322 influenced each faunal group by comparing the density and diversity (taxonomic richness) of  
323 each faunal group with the hydrological changes over time at each site. We fit five linear mixed

324 models to the data assuming five different distribution threshold (Fig. 2c), and compared their  
325 goodness of fit based on their Akaike information criterion (AIC) values. All models included a  
326 connectivity factor, described below, and habitat area as fixed effects, and block as a random  
327 effect, to control for inherent longitudinal habitat heterogeneity. The first model assumed a  
328 hydrological connection at flood peak (river connection on 15 May) influenced the biota, and  
329 included as binary factors Isolated sites versus all other sites. The second model assumed that  
330 the presence of flow at peak flood (on 15 May) influenced the biota, and included the binary  
331 factors Isolated+No\_flow sites versus other sites. The third and fourth models assumed that the  
332 timing of the flow cessation at each site influenced the biota. The third model assumed that the  
333 presence of flow on 23 May influenced the biota and included Isolated+No\_flow+Early sites  
334 versus Middle+Late+Flowing sites as binary factors. The fourth model assumed that the  
335 presence of flow on 28 May influenced the biota, and included  
336 Isolated+No\_flow+Early+Middle” sites versus Late+Flowing sites as binary factor. The final  
337 model assumed that the aquatic communities were structured primarily by the flow at the time  
338 of sampling, and included Flowing sites versus all other sites as binary factors. We fit these five  
339 models to the data on the total density of each respective faunal group and calculated the AIC  
340 value of each model. We then selected the model with the lowest AIC value as the best model  
341 for that faunal group. We analysed the diversity (taxonomic richness) of the four faunal groups  
342 similarly.

343

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

355

### 356 **3 RESULTS**

#### 357 **3.1 Physical environment**

358 The all 26 studied waterbodies ranged in width from 0.7 m to 2.9 m, in length from 4.7 m to 160  
359 m, and in depth from 0.08 m to 0.54 m at the time of the post-flood survey (i.e., after the

360 snowmelt flooding). Bottom sediment composition differed among the waterbodies depending  
361 on connectivity to the main stream; more connected sites had a lower proportion of organic  
362 sediments and contained larger rocks. Width, depth, and water velocity at the four focal sites  
363 gradually decreased as the river discharge decreased over the study period.

364

### 365 **3.2 Water chemistry**

366 The multivariate analysis of the water chemistry data collected during flood-recession and post-  
367 flood surveys revealed a link between the spatial and temporal water chemistry patterns. PCA1  
368 explained 42% of the total variation in the chemistry data (Fig. 3) and was inferred to represent  
369 temporal changes in habitat characteristics (ANOVA,  $F_{1,29} = 70.3$ ,  $P < 0.05$ ). Sites with different  
370 degrees of connectivity were arranged along PCA1 such that more isolated sites exhibited lower  
371 scores (ANOVA,  $F_{5,13.5} = 4.6$ ,  $P < 0.05$ ). Over the course of the flood-recession survey,  
372 conductivity and  $\text{NH}_4^+$  increased, and pH, DO, and  $\text{NO}_3^-$  decreased, but temporal changes in  
373 SRP were not significant. The spatial data showed that pH and DO were lower at more isolated  
374 sites, but connectivity was not significantly related to conductivity,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , or SRP.

375

### 376 **3.3 Flood-recession survey**

377 Quantities of both phytoplankton and zooplankton increased as the flood receded (Fig. 3).  
378 Chlorophyll-*a*, an indicator of phytoplankton density, significantly increased as the flood  
379 receded (ANOVA,  $F_{1,23} = 8.16$ ,  $P < 0.05$ ). During the flood-recession zooplankton survey, a  
380 total of 3407 copepods, 47 other crustaceans, and 105 mosquito larvae were counted. Total  
381 zooplankton density also increased significantly as the flood receded (ANOVA,  $F_{1,23} = 4.38$ ,  $P <$   
382  $0.05$ ).

383

384 In the fish survey, a total of 89 and 159 individuals were collected on 22 May and on 12 June  
385 2019, respectively, at the four focal sites (Fig. 4). Young-of-the-year charr and trout were  
386 recruited to the sampling sites over time; they were found only on the 12 June survey and only  
387 at sites C and D, where flow had occurred at peak discharge but had ceased by 6 June. Overall,  
388 fish species composition at the four sites did not differ significantly from before to after the  
389 flood, and variation in fish species among sites persisted. The PERMANOVA analysis showed  
390 that the spatial variation was greater than the temporal variation; the temporal change in fish  
391 species composition was not statistically significant (Table S1).

392

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

396

### 397 **3.4 Stable carbon isoscape**

398  $\delta^{13}\text{C}$  values of benthic macroinvertebrates and fish varied among the sites (Fig. 5; Fig. S1).  $\delta^{13}\text{C}$   
399 values of benthic macroinvertebrates were lower at sites with low connectivity (Spearman's rank  
400 correlation test;  $P < 0.05$ ,  $\rho = 1$ ). At the No flow sites A and B, they ranged from  $-42\text{‰}$  to  $-33\text{‰}$   
401 and from  $-43\text{‰}$  to  $-33\text{‰}$ , respectively, and at sites C (Middle) and D (Late), they ranged from  $-$   
402  $35\text{‰}$  to  $-31\text{‰}$  and from  $-31\text{‰}$  to  $-27\text{‰}$ , respectively; at site E (on the main stream), they ranged  
403 from  $-30\text{‰}$  to  $-25\text{‰}$ .  $\delta^{13}\text{C}$  values of fish were positively correlated with those of benthic  
404 macroinvertebrates at each site ( $Y = 0.81x - 1.86$ ,  $R^2 = 0.95$ ,  $P < 0.01$ ). They ranged from  $-36\text{‰}$   
405 to  $-32\text{‰}$  at site A, from  $-34\text{‰}$  to  $-29\text{‰}$  at site B, from  $-39\text{‰}$  to  $-25\text{‰}$  at site C, from  $-25\text{‰}$  to  
406  $-24\text{‰}$  at site D, and from  $-25\text{‰}$  to  $-25\text{‰}$  at the site E.

407

### 408 **3.5 Post-flood survey**

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

414

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

421

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

429

430 Only two species of amphibians, *Rana pirica* and *Hynobius retardatus*, were observed during  
431 the present study. The model comparison showed that the presence of amphibian eggs was best

432 explain by flow cessation on 23 May (and secondarily by flow on 28 May) (Table 1); thus, the  
433 timing of flow cessation determined whether eggs of these amphibian species were present.

434

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

445

#### 446 **4 DISCUSSION**

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

460

461 The temporal dynamics of nutrient concentrations and phyto- and zooplankton over the flood  
462 recession period showed that plankton bloomed in isolated waterbodies never flushed by  
463 flowing floodwaters, and that the nutrients became depleted in such isolated waterbodies over  
464 time. The lower nutrient concentrations ( $\text{NO}_3^-$  and SRP) in waterbodies with high densities of  
465 phyto- and zooplankton indicate that plankton density was limited by factors other than nutrient  
466 availability, and that in isolated waterbodies nutrients were depleted by plankton (Van Den  
467 Brink et al., 1992). Plankton communities are known to be vulnerable to flow (Chaparro et al.,

468 2018; Van den Brink et al., 1994); thus, in many of the waterbodies, phyto- and zooplankton  
469 were likely flushed by the floodwaters. However, the emergence of plankton in waterbodies that  
470 had been flushed indicates that some plankton somehow remained in these waterbodies during  
471 the flood period (Frisch, 2002) or that they colonized them after the flood (Jenkins & Boulton,  
472 2003). Although in each waterbody the plankton density started to increase once the flow  
473 stopped, and it is possible that later in the low-flow season (i.e., after the study period) their  
474 density would become higher (Baranyi et al., 2002; Grosholz & Gallo, 2006; Schagerl et al.,  
475 2009), their recovery was not fast enough to compensate for the impacts of the flow at flood  
476 peak by the time of sampling.

477

478 In contrast to plankton, fish were more abundant and diverse in waterbodies that were flushed  
479 by the peak flow. The spatial match between the stable carbon isotope ratios of fish fry and  
480 benthos, together with the similarity of the fish species composition at each site between the  
481 flood-recession and post-flood surveys, indicates that the residency of fish fry in each palaeo-  
482 side channel was high. Salmonids spawn in habitats with gravel and pebble substrates  
483 (Montgomery et al., 1999), which are common in the main stream and side channels of the  
484 studied system. Furthermore, most of the fish in the floodplain waterbodies (palaeo-side  
485 channels) were juveniles; adults were found only in the main stream. Fitzgerald et al. (2021)  
486 estimated that the dominant species in the studied system, *Oncorhynchus masou* and *Salvelinus*  
487 *leucomaenis*, hatch primarily in February and March. Therefore, it is assumed that salmonid fry  
488 that hatched in extant side channels or the main stream of the river moved to the palaeo-side  
489 channels during the flood to continue their development as described by Rosenfeld et al.,  
490 (2008), whereas those hatched in extant side channels during the summer low-flow period  
491 remained there during their development. Floodplain waterbodies are important nurseries for  
492 many fishes in the river (Jeffres, Opperman & Moyle, 2008; Bellmore et al., 2013), and they  
493 out-migrate from side channels to the river and sometimes to downstream lakes as they grow  
494 (Tamate & Maekawa, 2004; Kanno et al., 2020). Although fish diversity was lower in  
495 waterbodies with lower connectivity, we observed some fish species in those waterbodies that  
496 were not found in the more connected waterbodies. Species that occurred in isolated  
497 waterbodies included Cyprinidae and Cobitidae, which are known to tolerate anoxic conditions  
498 (Fagernes et al., 2017). The spatial variation in hydrological dynamics over flood recession  
499 period thus contributed to the diversity of fish fauna on the floodplain.

500

501 Interestingly, the presence of amphibians was determined by the timing of flow cessation in  
502 each waterbody. Both amphibian species reproduced in the floodplain waterbodies soon after  
503 the flood peak, and their eggs hatched and larvae developed in the waterbodies during the low-

504 flow period, a common pattern in amphibians (Griffiths, 1997; Tockner et al., 2006; Holgerson  
505 et al., 2019). Our post-flood survey showed that amphibian eggs were laid and larvae were  
506 observed in waterbodies where the flow had stopped in the early flood recession period, before  
507 their reproductive season. Waterbodies on the floodplain provide important habitats for  
508 amphibian larvae, yet use of this temporary habitat exposes them to various risks, including  
509 desiccation (Gervasi & Foufopoulos, 2008) and being flushed by flow (Indermaur et al., 2010).  
510 Therefore, the timing of environmental shifts such as flood recession may be particularly  
511 important for amphibians, which use the floodplain waterbodies only seasonally.

512  
513 Finally, benthos distributions were greatly influenced by the occurrence of flow at the time of  
514 sampling. We observed diverse aquatic insect taxa, including Ephemeroptera, Plecoptera, and  
515 Trichoptera, in flowing waterbodies; most of these taxa require flowing water for respiration  
516 (Merritt, Cummins & Berg, 2008), and they were not found in more isolated floodplain  
517 waterbodies. In contrast, Chironomidae dominated most of the floodplain waterbodies in this  
518 study. Relatively low Chironomidae density in isolated waterbodies, which were not flushed by  
519 flow at peak flood, in contrast to other floodplain waterbodies may be explained by the  
520 extremely anoxic conditions of benthic habitats in those waterbodies. The low  $\delta^{13}\text{C}$  ( $-40\text{‰}$ ) of  
521 benthos in isolated waterbodies indicates that benthic conditions were so anoxic that methane-  
522 derived carbon was consumed by the benthos (Kohzu et al., 2004). In this study, we sorted  
523 benthos at the family level, but species level identification could have shown spatial variation of  
524 Chironomidae according to the hydrological dynamics over flood.

525  
526 Overall, the observed unique responses of the four faunal groups to the hydrological dynamics  
527 over the snowmelt flood recession period well explained the spatial distributions of the four  
528 faunal groups on a floodplain. This indicates spatial asynchrony in channel isolation from the  
529 main stream during flood recession and responses of the four biological groups led their distinct  
530 distributions on a floodplain. We however acknowledge the difficulties in clearly teasing out the  
531 effect of spatial variation in hydrological dynamics over the flood recession period we focused  
532 in this study from the effect of spatial variations in local environmental conditions (such as  
533 dissolved oxygen, pH, and substrate type). Future experimental studies would be required to  
534 clearly distinguish among these factors. Furthermore, the four faunal groups that are  
535 individually presented in this study interact with each other through food webs. Diverse aquatic  
536 communities on the floodplain observed in this study indicate that food web structures are also  
537 variable. Further studies of community structures and species interactions in relation to  
538 hydrological dynamics would provide insights into the dynamic meta-community (Leibold et  
539 al., 2004) and meta-ecosystem structures (Gounand et al., 2018) on a floodplain.



540

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

554

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

567

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583

#### 584 **Conflicts of Interest Statement**

585 The authors declare no conflict of interest.

586

#### 587 **Data Availability Statement**

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

590

#### 591 **Legends**

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

594

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

600

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

608

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

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

615

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

620

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

625

626 Figure 6: Spatial variation of density and diversity of the four faunal groups in the post-flood  
627 sampling. Each bar indicates the average density of each faunal group at multiple sites with the  
628 same connectivity to the river. Circles indicate the average taxa richness of each faunal group at  
629 multiple sites with the same connectivity. The error bars indicate  $\pm 1$  standard error among sites.  
630 Black inverted triangles indicate primary and secondary ( $\Delta\text{AIC} < 4$ ) thresholds of faunal  
631 density, and white inverted triangles indicate the thresholds of faunal diversity based on the  
632 model selection results shown in Table 1.

633

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

641

642

643

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

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

808 Table1

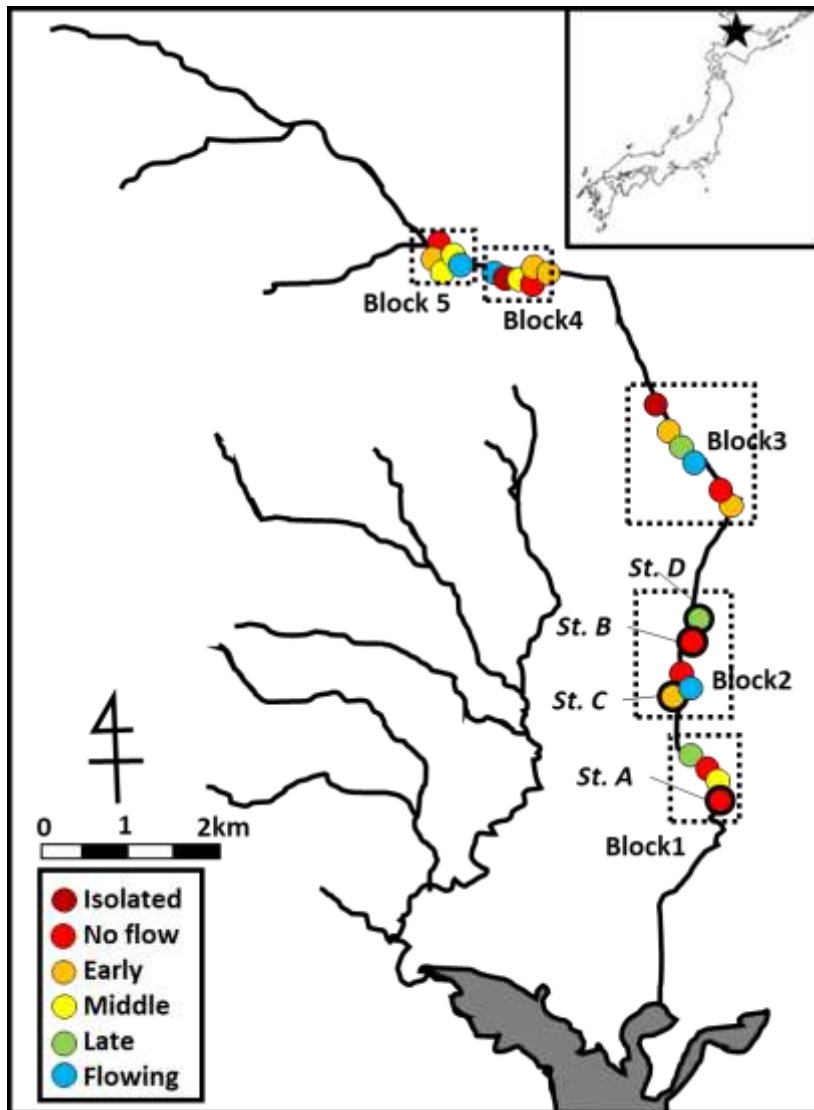
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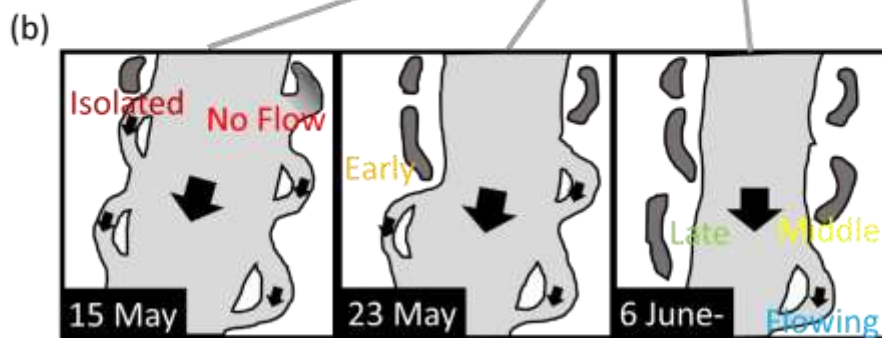
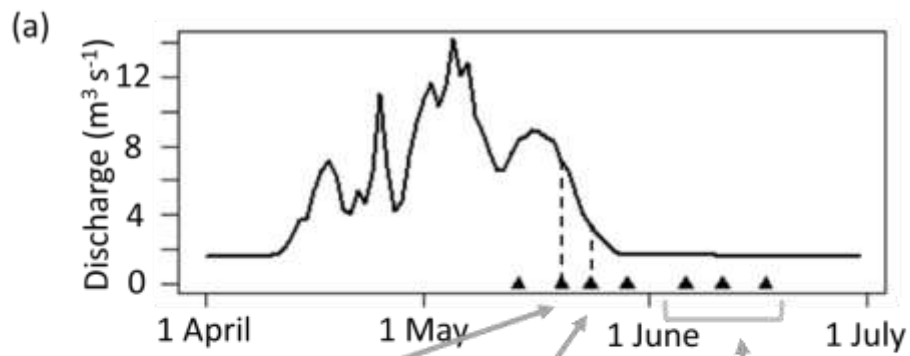
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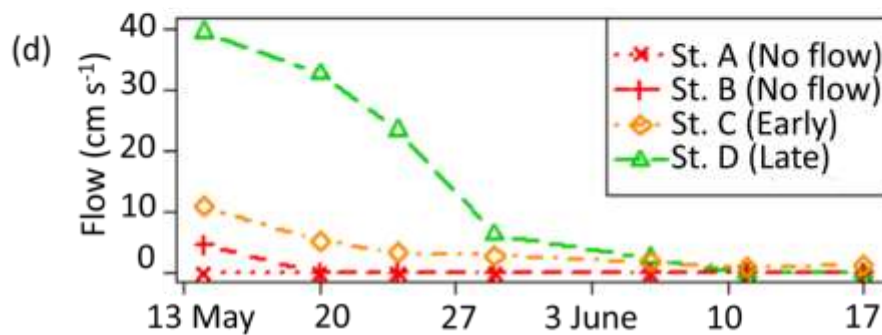
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815 Figure1



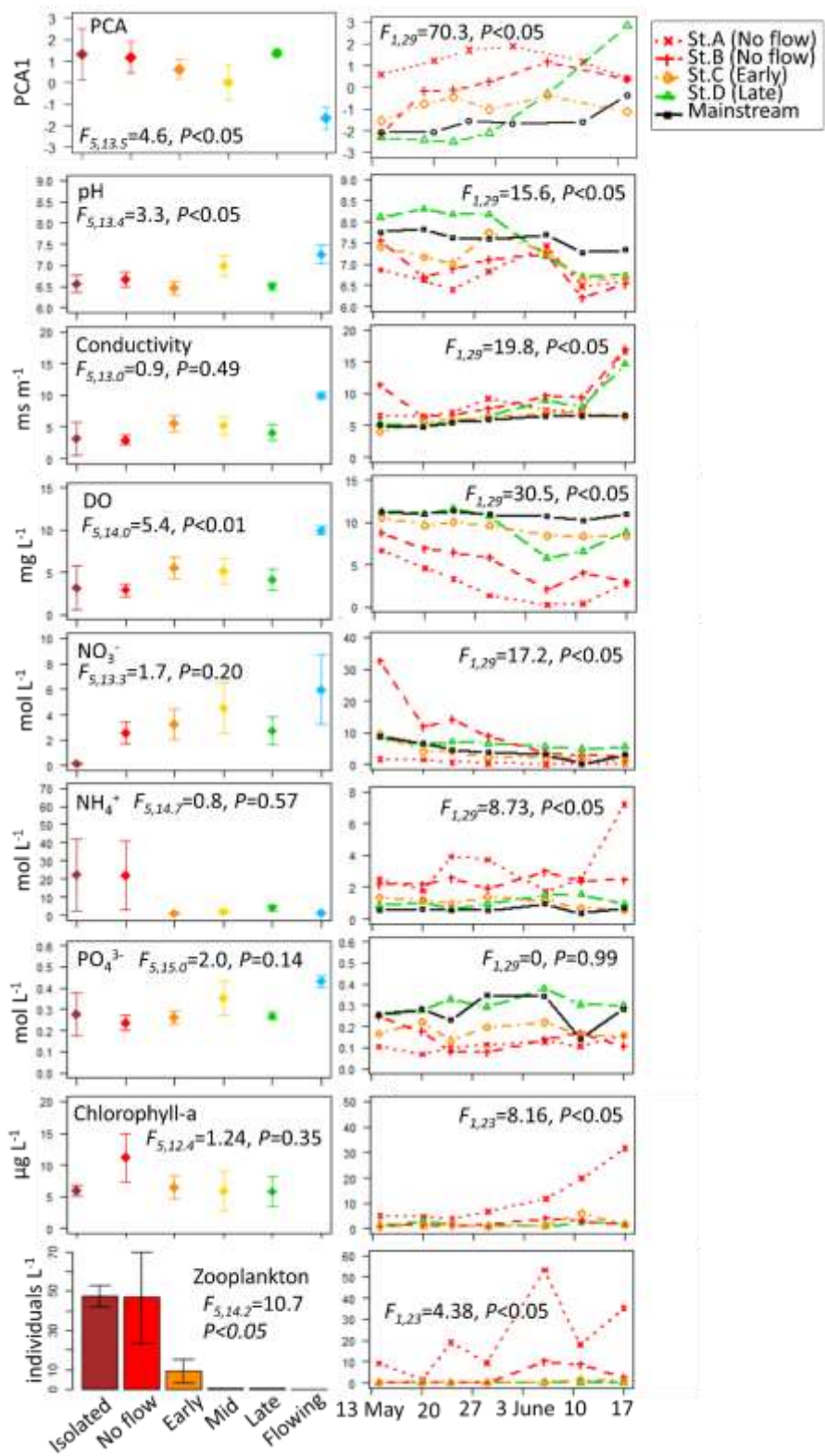
(c)

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	×	×	×	×	×	×



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817 Figure 2

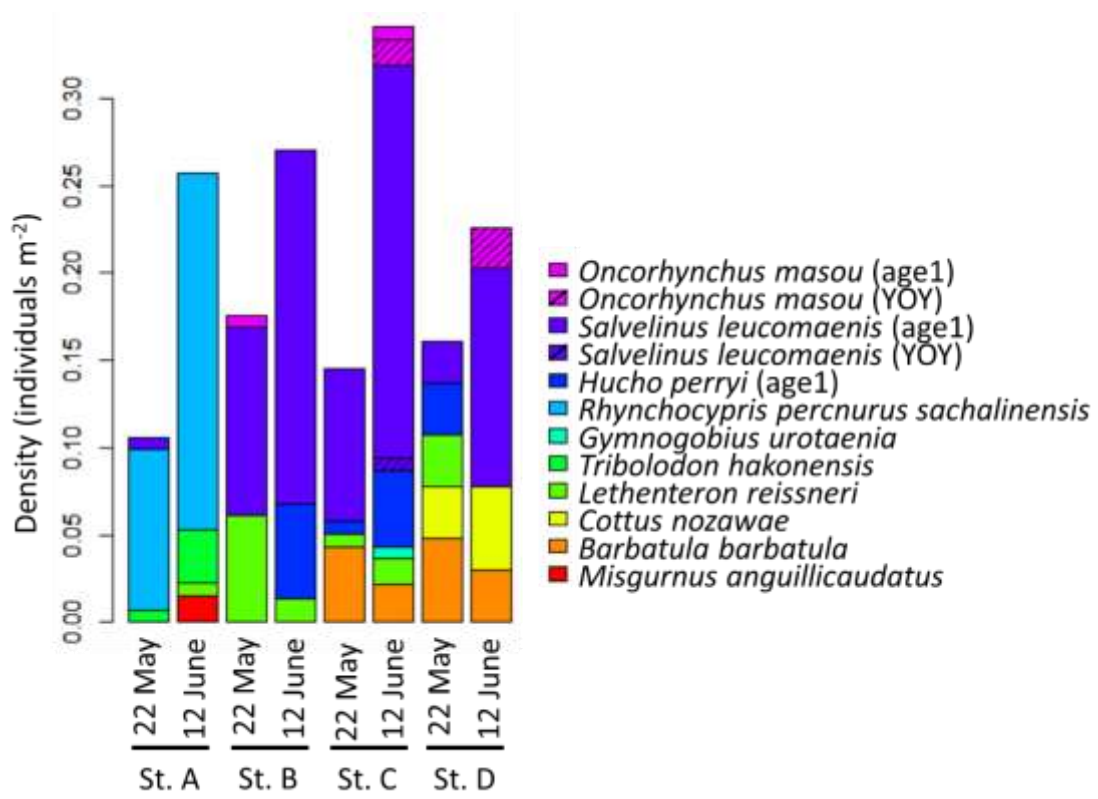


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819 Figure 3

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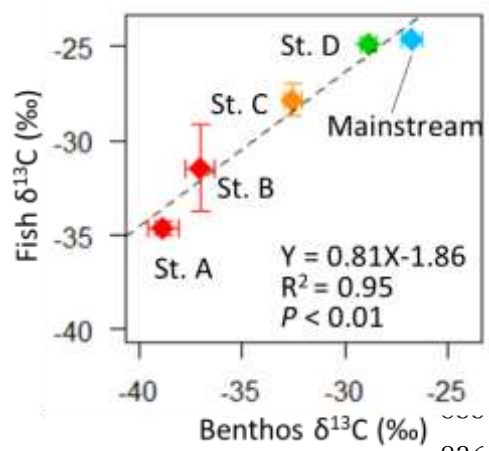
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824 Figure 4

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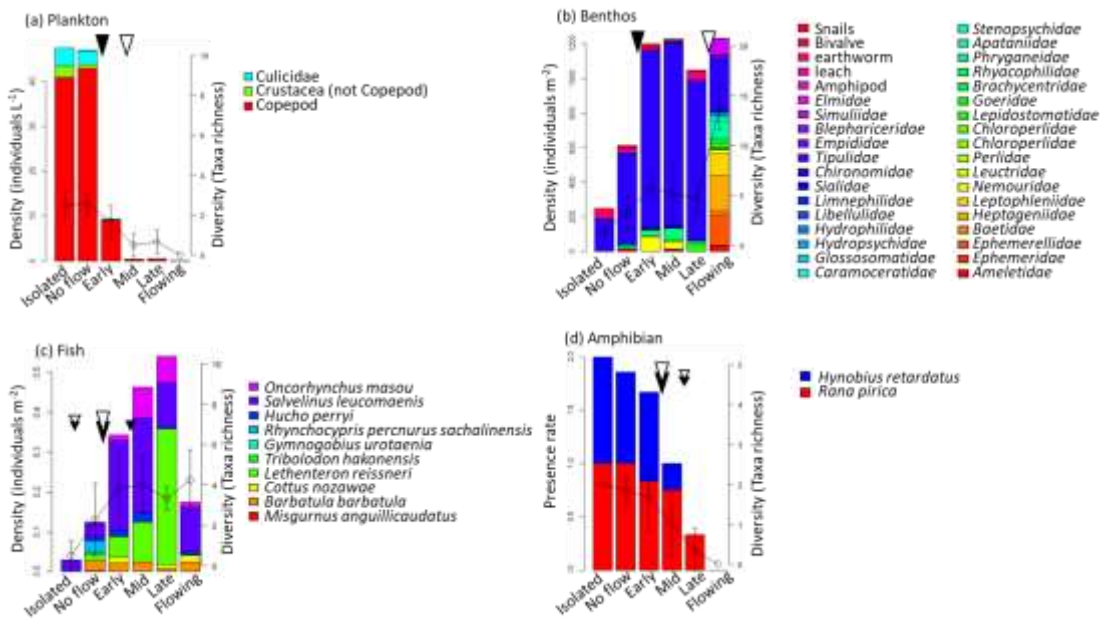
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838 Figure 5

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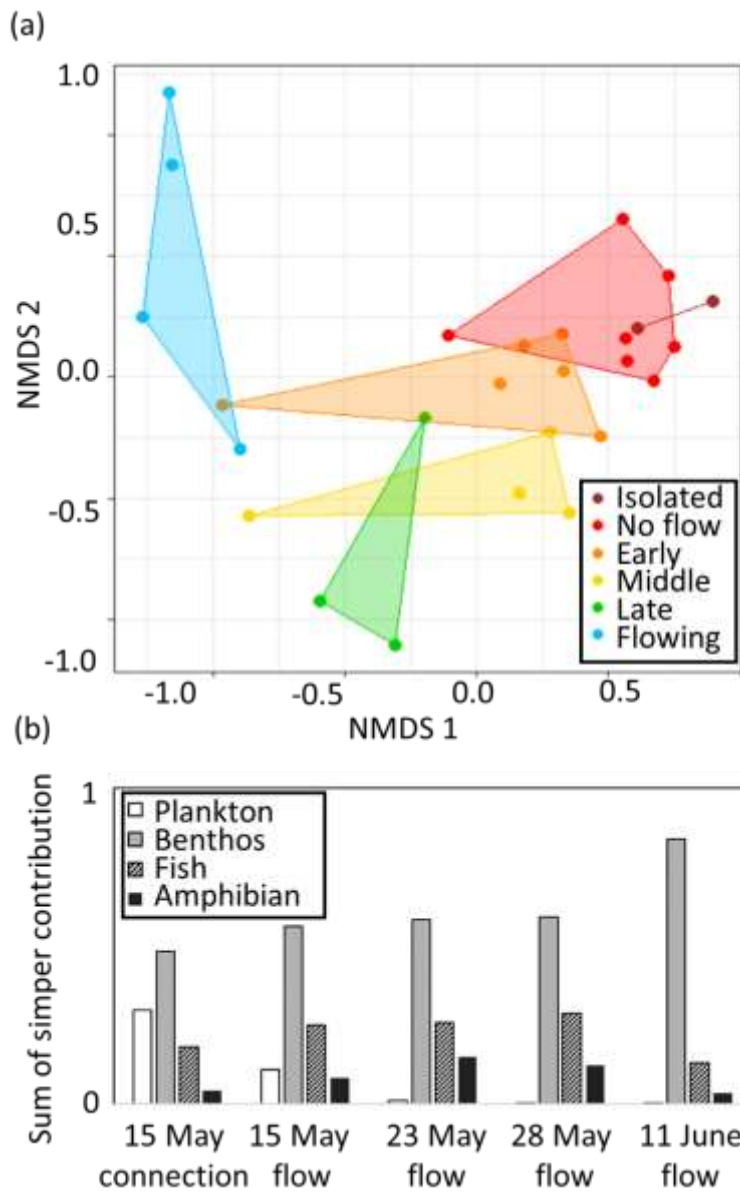


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843 Figure 6

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847 Figure 7

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